# ELEMENTS

OF THE

# COMPARATIVE ANATOMY

OF

# VERTEBRATES

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# VERTEBRATES

ADAPTED FROM THE GERMAN OF

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### SECOND EDITION

(FOUNDED ON THE THIRD GERMAN EDITION)

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# PREFACE TO THE FIRST EDITION

PROFESSOR WIEDERSHEIM'S *Grundriss der vergleichenden Anatomie der Wirbelthiere*, published at Jena in 1884, was written to supply a need which had been felt for some time past for a short text-book on Vertebrate Anatomy embodying some of the more recent views on the subject. The present book is a modified translation of the *Grundriss*, and it is hoped that it will serve to render Professor Wiedersheim's work more widely known amongst English students.

The plan of the original has been retained throughout, though numerous additions and modifications have been made to the work ; for many of these I have to thank Professor Wiedersheim,—for others I am myself responsible. I must also express my indebtedness to Professor Wiedersheim for revising the whole translation with me last summer, and for much help while the work was in progress.

Within the limits of a short text-book like the present, much of the matter is of necessity greatly condensed : more detailed accounts of the various parts and organs will be found in the new edition of Professor Wiedersheim's *Lehrbuch der vergl. Anatomie der Wirbelthiere*, which is to appear shortly, and on the first edition of which the *Grundriss* was founded.

The brevity of the descriptions is, however, to some extent made up for by the number of woodcuts. Most of these are taken from the German edition, but several new figures have been added.

The arrangement of the book according to organs, and not according to groups of animals, is likely to render it more difficult for a beginner, and a general knowledge of Zoology will be of great assistance. The pages on which the different groups are described are, however, collected together in the index, so that the sections relating to any one group can be easily referred to. The present arrangement seems to be the only possible one if the book is to be founded on a scientific basis, for it is most important that the student should grasp the fact that there has been an evolution of organs, as well as of animals.

The more theoretical and detailed matter is printed in small type, and in the form of notes : the student should in most cases pass this over when reading the book for the first time. A black and a spaced type have been used to render prominent important words or sentences.

A bibliography is appended at the end of each chapter. This in no case presumes to be anything like a complete list of the literature of the subject: our object has been more particularly to mention the recent and the more important works, though many of these have doubtless been omitted. References to other researches can be found by consulting the works mentioned.

At Professor Wiedersheim's suggestion, I have not inserted a translation of the preface to the original, as it seemed unnecessary so to do. I may, however, mention that the book was written for students of Medicine, as well as for those of Comparative Anatomy : the intimate connection of the two subjects renders it most

important that medical students should have a general scientific basis for their special anatomical knowledge.

My sincerest thanks are due to my friends Professors F. Jeffrey Bell and G. B. Howes, who have kindly read through the proof-sheets. To them I am indebted for numerous valuable suggestions, as well as for correcting many faults of style and expression which had escaped my notice. I must also express my thanks to my father, Professor W. K. Parker, and to Dr. Gadow, for many special details in connection with the skeleton, as well as to Mr. E. Radford for help in making the index.

<div align="right">W. N. PARKER.</div>

University College, Cardiff,
    *May*, 1886.

# PREFACE TO THE SECOND EDITION

SINCE the publication of the first edition of the *Grundriss*, on which the first English edition was founded, two further German editions have appeared, one in 1888 and another in 1893, the latter containing 695 pages as compared with 272 pages in the first edition. The book has, in fact, grown beyond the limits of a "*Grundriss*," and has replaced the original *Lehrbuch*, no new edition of which has appeared since 1886.

As it seemed desirable that the second English edition should be brought up to date without greatly exceeding the limits of the first, it has been necessary to use a free hand in abridging and recasting the text. I have therefore, with the author's permission, attempted to prepare a short text-book which, while retaining the original descriptions and arrangement as far as possible, should deal with the more essential and well-ascertained facts of Comparative Anatomy, presenting an approximate equality of treatment as regards its different sections without entering too fully upon doubtful theories or special details in Embryology and Physiology.

The book has thus been almost entirely rewritten, with the approval of Professor Wiedersheim, who, besides revising the work, has furnished me with much new material. A number

of the old figures have been replaced and several additional ones inserted.

The bibliography appended to the book, which has been considerably added to by Professor Wiedersheim since the third German edition was published, is rather extensive for a work of the kind, but I have not ventured to make selections from it and have merely modified the arrangement in some respects and made a few additions which seemed to me important for English readers.    It will, I trust, be found useful by more advanced students.

I must acknowledge my obligations to my brother, Professor T. Jeffery Parker, F.R.S., for numerous suggestions, and also to Professor G. B. Howes, F.R.S., Mr. Frank J. Cole, and Mr. Martin F. Woodward for valuable information on several special points.

W. N. PARKER.

UNIVERSITY COLLEGE, CARDIFF,
    *April*, 1897.

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# COMPARATIVE ANATOMY

## INTRODUCTION.

A KNOWLEDGE of the natural relationships and ancestral history
of animals can only be gained by a comparative study of their
parts (**Comparative Anatomy**) and of their mode of develop-
ment (**Embryology** or **Ontogeny**).   In addition to existing
animals, fossil forms must also be taken into consideration ( **Pa-
læontology**), and by combining the results obtained under these
three heads, it is possible to make an attempt to trace out the
development of the various races or groups in time (**Phylogeny**).
As the different phases of development of the race may be repeated
to a greater or less extent in those of the individual, the depart-
ments of Ontogeny and Phylogeny help to complete one another.

It must, however, be borne in mind that in many cases the
phases of development are not repeated accurately in the individual
—that is, are not *palingenetic*,—but that "falsifications" of the re-
cord, acquired by adaptation, very commonly occur along with
them, resulting in *cænogenetic* modifications in which the original
relations are either no longer to be recognised at all, or are more
or less obscured.   In this connection, two important factors must
be taken into consideration, viz., *heredity* and *the capability of
variation*.   The former is conservative, and tends to the retention
of ancestral characters, while the latter, under the influence of
change in external conditions, results in modifications of structure
which are not fixed and unalterable, but are in a state of constant
change.   The resulting "*adaptations*," so far as they are useful to
the organism concerned, are transmitted to future generations,
and thus in the course of time gradually lead to still further
modifications.   Thus *heredity and adaptation are parallel factors*,
and a conception of the full meaning of this fact helps us not only
to gain an insight into the blood-relationships of animals in gene-
ral, but also to understand the meaning of numerous degenerated

and rudimentary or vestigial organs and parts in the adult organism which would otherwise remain totally inexplicable.

**Histology** is a subdivision of anatomy which concerns the *structural elements*—the building-stones of the organism, and the combination of these to form **tissues.** Various combinations of the tissues give rise to **organs**, and the organs, again, combine to form **systems of organs.**

The structural elements consist primarily of **cells** and secondarily of *cells* and *fibres*, and the different tissues may be divided into four principal groups :—

1. **Epithelium**, and its derivative, **glandular tissue.**
2. **Supporting-tissue** (connective-tissue, cartilage, bone).
3. **Muscular tissue.**
4. **Nervous tissue.**

In accordance with the functions they perform, epithelium and supporting-tissue may be described as *passive*, and muscular and nervous tissue as *active*.

By an *organ* we understand an apparatus constructed to perform a definite function : as, for instance, the liver, which secretes bile ; the gills and lungs, in which an exchange of gases is effected with the surrounding medium ; and the heart, which pumps blood through the body.

The *organ-systems*, which will be treated of in order in this book, are as follows :—1. The outer covering of the body, or *integument ;* 2. The *skeleton ;* 3. The *muscles*, together with *electric organs ;* 4. The *nervous system* and *sense-organs ;* 5. The organs of *nutrition, respiration, circulation, excretion,* and *reproduction.*

The closely-allied branches of science defined above are united together as **Morphology,** as opposed to **Physiology** which concerns the functions of organs, apart from their morphological relations. The results obtained from these two fields of study help to complete one another, and thus to throw light on the organisation of animals in general—that is, on **Zoology** in its widest sense.

## II. DEVELOPMENT AND STRUCTURAL PLAN OF THE VERTEBRATE BODY.

The structural elements described in the preceding section as the building-stones of the organism, *i.e.* the cells, all arise from a *single primitive cell*, the **egg-cell** or **ovum.** This forms the starting-point for the entire animal-body, and a general account of its structure and subsequent development must therefore be given here.

The ovum consists of a rounded vesicle (Fig. 1), in the interior of which the following parts can be distinguished :—the *vitellus,*

the *germinal vesicle*, and one or more *germinal spots*. The outer covering of the ovum is spoken of as the *vitelline membrane.*

Since the ovum in its primitive form as above described represents a single cell, we may speak of the vitellus [1] as the *protoplasm* of the egg-cell, the germinal vesicle as its *nucleus*, and the germinal spot as its *nucleolus.* The cell-nucleus is enclosed by a delicate nuclear membrane, and is made up of two constituents—the *spongioplasm* or *chromatin*, and the *hyaloplasm* or *achromatin.* One or two small particles, the *centrosomes*, are also present in the cell-body, and take an important part in the process of cell-division. An outer limiting membrane, corresponding to the vitelline membrane, is not an integral part of the cell, but may be differentiated as a hardening of the peripheral protoplasm.

In **sexual reproduction,** such as occurs in all Vertebrates, the fusion of the **sperm-cell**, containing the generative substance of the male, with the ovum, is an absolute necessity for the development of the latter.



FIG. 1.—DIAGRAM OF THE UNIMPREGNATED OVUM.

*D*, vitellus ; *KB*, germinal vesicle ; *KF*, germinal spot.

But before this can occur, certain changes take place in the ovum, which are known as **maturation.** This consists of a twice-repeated process of cell-division (*karyokinesis*) similar to that which occurs in tissue-cells, except that the resulting daughter-cells are of different sizes, two small nucleated *polar-cells* (Fig. 2) being successively thrown off from the larger ovum, the portion of the original nucleus remaining in the ovum being known as the "*female pronucleus.*" A *sperm-cell* (*spermatozoon*) then makes its way into the ovum, and its nucleus (the *male pronucleus*) unites with the female pronucleus to form the **segmentation nucleus.** This process, which is known as **impregnation** or **fertilisation,** thus consists in a *material fusion of the generative substances of both sexes*, or more accurately of *the sperm-nucleus and egg-nucleus.* The essential cause of inheritance can thus be traced to the molecular structure of the nuclei of both male and female germinal cells. This structure is the morphological expression of the characters of the species.

After fertilisation has taken place **development** begins. The segmentation nucleus divides into two equal parts, each of which forms a new centre for the division of the **oosperm,** as it must now be called, into two halves or *blastomeres.* This division, the beginning of the process of **segmentation,** takes place by the formation of a furrow round the egg which becomes deeper and deeper until the division is complete. (Fig. 2, A).

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[1] The vitellus consists of two different substances—*protoplasm* and *deuteroplasm* (*yolk*)—in varying proportions in different animals.

The first stage in the process of segmentation is thus completed; the second takes place in exactly the same way, and results in a division of the oosperm into four parts, and by a similar process are formed eight, then sixteen, then thirty-two blastomeres, and so on, the cells becoming smaller and smaller, and each being provided with a nucleus (Fig. 2 C—D). In short, out of the original oosperm a mass of cells is formed which represents the building-material of the animal body and which, from its likeness in appearance to a mulberry, is spoken of as a **morula.**

In the interior of the morula a cavity (*segmentation cavity* or
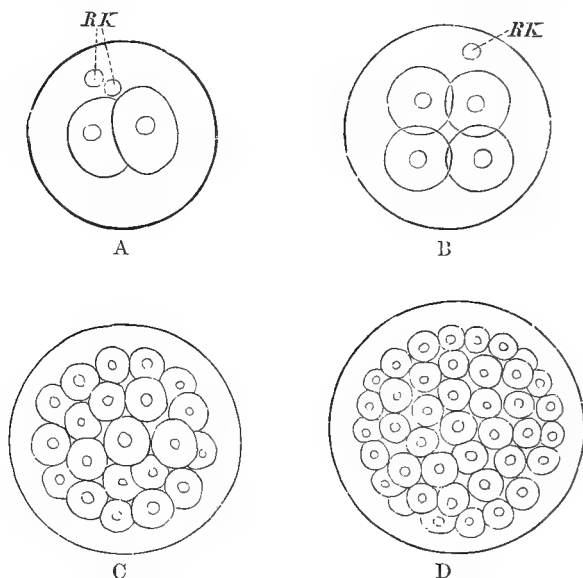


Fig. 2.—Diagrams of the Segmentation of the Oosperm.

A, first stage (two segments): *RK*, polar cells. B, second stage (four segments). C, further stage. D, morula stage.

*blastocœle*) filled with fluid is formed, and the morula is now spoken of as the **blastosphere** or **blastula** (Fig. 3). The peripheral cells enclosing this cavity form the **germinal membrane** or **blastoderm.** Consisting at first of a single layer of cells, the blastoderm later on becomes two- and then three-layered. From the relative positions of these, they are spoken of respectively as the *outer*, *middle*, and *inner* **germinal layers,** or as **epiblast, (ectoderm,) mesoblast, (mesoderm,)** and **hypoblast (endoderm).**

An increase in the amount of food-yolk (deuteroplasm, see note on p. 3) present in the ovum results in certain modifications of the primitive process of segmentation as described above. Yolk is an inert

substance, and its presence tends to hinder or even entirely to prevent segmentation in those parts of the ovum in which it is abundant. When the whole ovum undergoes division, the segmentation is known as *entire* or *holoblastic;* when division is restricted to part of the ovum only, the segmentation is said to be *partial* or *meroblastic* [1] (Fig. 4).

The question as to the origin of the germinal layers, on account of its important signification, is one of the most burning problems in Morphology, and as yet we cannot arrive at any full and satisfactory conclusion on the subject. It may, however, be affirmed with certainty that in all Vertebrates the blastosphere passes—or did so in earlier times—into a stage called the **gastrula.** One



FIG. 3.—BLASTOSPHERE.

*BD*, blastoderm ; *FH*, segmentation cavity.

must imagine this form as being derived primitively from the blastula by supposing that the walls of the latter (Fig. 3) became pushed in or invaginated at one part, thus giving rise to a double-walled sac (Fig. 5). The outer wall then represents the epiblast, which functions as an organ of protection and sensation, while the inner, or hypoblast, encloses a central space, the *primitive intestinal cavity* (**archenteron**), and represents the assimilating and digestive primary alimentary canal. The opening of the latter to the exterior, where the two germinal layers are continuous, represents the *primitive mouth* or **blastopore** (Fig. 5).



FIG. 4.—DIAGRAM OF A MEROBLASTIC OOSPERM WITH DISCOID SEGMENTATION.

*Bla,* blastoderm ; *Do,* yolk.

Out of the *epiblast* arise later the epidermis and its derivatives, the entire nervous system, the sensory cells, the crystalline lens of the eye, and the oral and anal involutions (*stomodœum* and *proctodœum*). In an early stage the *hypoblast* gives rise to an axial rod, the *notochord* (see p. 9), and eventually to the epithelium of the greater part of the alimentary canal

[1] In holoblastic segmentation the resulting cells are approximately *equal* in the Lancelet and in Mammals (with the exception of Monotremes) ; and *unequal* in the Cyclostomes, Sturgeon, Lepidosteus, Ceratodus, and nearly all Amphibians, the segmentation sometimes approaching the meroblastic type. In Elasmobranchs, Teleosts, Reptiles, Birds, and Monotremes the segmentation is meroblastic and *discoid*, *i.e.*, restricted to the upper pole of the ovum (Fig. 4).

(Fig. 6, A and B) with its glands, including the thyroid, thymus, liver and pancreas, as well as to the epithelial parts of the gill-sacs and lungs.

Though we may look upon the epiblast and hypoblast,—that is, both the primary germinal layers—as arising in the manner above described, the problem as to the origin of the *mesoblast* is as yet by no means settled. All that can be said at present is briefly as follows :—The mesoblast is a secondary formation, and is phylo-genetically younger than the other two germinal layers ; both as regards the origin of its cells and histologically, it is of a com-pound nature, and thus forms a marked contrast to the germinal layers proper. Reminding one in many points of the " *mesenchyme* " of Invertebrates, it always arises at first from the point where
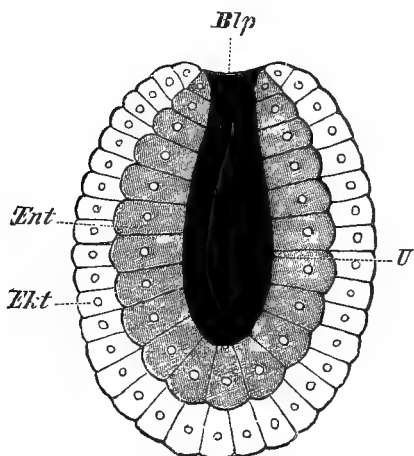


FIG. 5.—GASTRULA.

*Ekt*, epiblast ; *Ent*, hypoblast ; *Blp*, blastopore ; *U*, archenteron.

epiblast and hypoblast pass into one another, that is, from the region of the blastopore, or, what comes to the same thing in the higher Vertebrates, from the *primitive streak*. Originating from between the other two layers, one of its first and most important functions is the formation of *blood-cells* ; later it gives rise to the *heart, vessels, supporting* and *connecting substances* (connective-tissue, adipose tissue, cartilage, and bone), *serous membranes* (peritoneum, pleura, pericardium, arachnoid), *muscles*, and almost the entire *excretory* and *reproductive apparatus*.

A cleft appearing in the mesoblastic tissue divides it into a *parietal* or *somatic layer* (Fig. 6, A and B), lying along the inner side of the epiblast, and into a *visceral* or *splanchnic layer*, which becomes attached to the outer side of the hypoblast. The former, together with the epiblast to which it is united, constitutes the
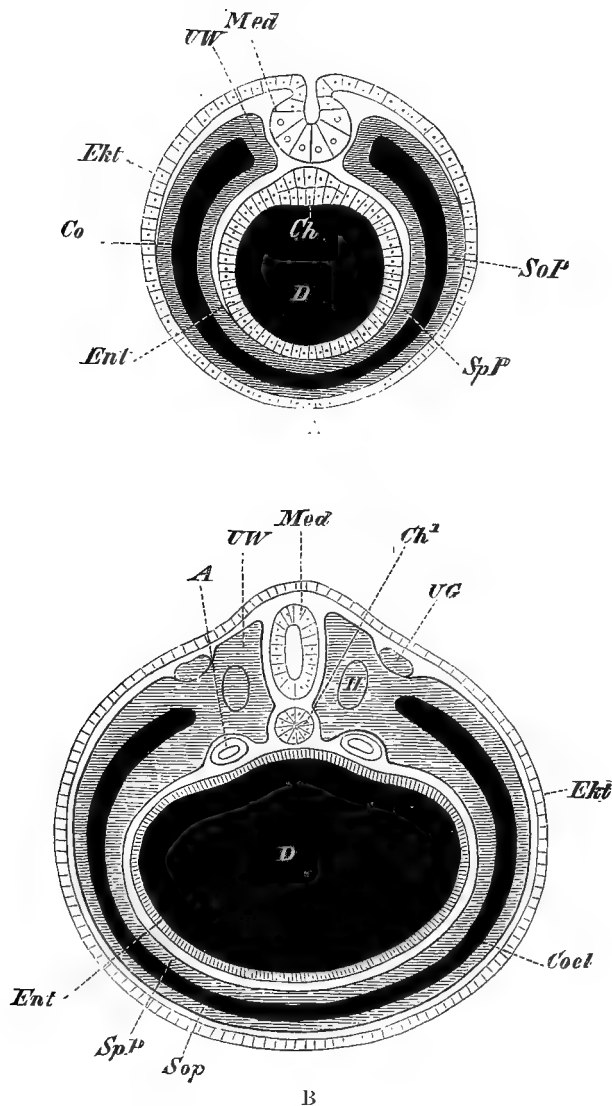
FIG. 6, A AND B.—DIAGRAMMATIC TRANSVERSE SECTIONS THROUGH A DEVELOPING VERTEBRATE EMBRYO.

*D*, alimentary canal ; *Ent*, hypoblast, showing in Fig. A the thickening (*Ch*) which will form the notochord ; *Ch*[1] (Fig. B), the notochord now constricted off from the hypoblast ; *UW*, mesoblastic somite ; *UG*, primary urinary duct (pronephric duct) ; *A*, aorta ; *SpP*, splanchnic and *Sop*, somatic mesoblast ; *Co*, *Cœl*, cœlome ; *H*, remains of the upper part of the cœlome in the interior of the mesoblastic somites ; *Ekt*, epiblast ; *Med*, central nervous system (medullary cord) :—in Fig. A it is shown still connected with the epiblast, from which it has become constricted off in Fig. B.

*somatopleure,* and the latter, together with the hypoblast, the *splanchnopleure.* The cavity separating these is the body cavity, or **cœlome** (Fig. 7),[1] and is lined by an epithelium. The dorsal part of the mesoblast which lies on either side of the middle line early becomes transversely segmented to form a series of *mesoblastic somites* or *protovertebræ,* which lose their cavities (Fig. 6, A and B) and are concerned in the formation of the vertebral column, body muscles, and urinogenital apparatus.

As a general rule a thickened disc-shaped region can be recognised at a certain stage of development on the dorsal pole of the
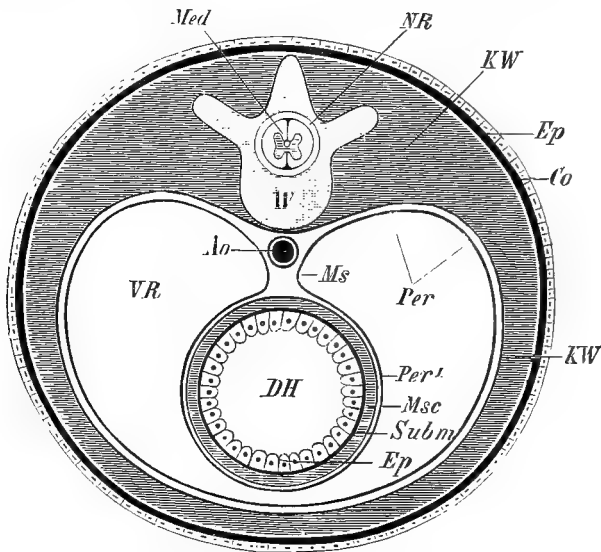


FIG. 7.—DIAGRAMMATIC TRANSVERSE SECTION THROUGH THE BODY OF AN ADULT VERTEBRATE.

*Med,* spinal cord ; *NR,* neural tube ; *KW,* body-wall ; *Co,* dermis ; *Ep,* endodermic epithelium of alimentary canal (intestine) ; *VR,* visceral tube ; *Ao,* aorta ; *Ms,* mesentery ; *Per,* parietal layer of the peritoneum ; *Per*[1], visceral layer of the peritoneum ; *Msc,* muscular coat of intestine ; *Subm,* connective-tissue coat of intestine ; *DH,* lumen of intestine ; *W,* vertebral centrum with dorsal arch.

oosperm : this is the so-called *embryonic area,* and on it the first indications of the body are seen. This region gradually becomes constricted off from the yolk by the formation of furrows at its anterior and posterior ends as well as laterally, and consequently the connection of the body-rudiment with the ventral *yolk-sac* (the

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[1] The cœlome may arise as a segmentally arranged series of pouches (*enterocœles*) from the archenteron, in which case its lining epithelium is at first continuous with the hypoblast, as is most plainly seen in Amphioxus ; or it may be formed secondarily by a splitting (delamination) of the mesoblastic tissue (*schizocœle*). The first of these must be considered as the more primitive.

*vitello-intestinal duct*) is reduced in size, and when the yolk is eventually entirely absorbed, disappears altogether (Fig. 8, †). In the higher Vertebrates (Reptiles, Birds, and Mammals) folds of the somatopleure arise externally to these furrows, and are known respectively as the *head*, *tail*, and *lateral folds*; these gradually grow upwards and eventually unite with one another dorsally so as to form a membranous, dome-like sac, the **amnion** (Fig. 8) which encloses the embryo and contains a fluid (*liquor amnii*).

Owing to the presence of this structure the above-named Vertebrates are usually distinguished as **Amniota** from the **Anamnia** (Fishes and Amphibians), in which no amnion is developed (p. 13).

A network of blood-vessels becomes developed over the yolk-sac, which may therefore serve as an organ of *respiration* as well as of nutrition. But in the higher Mammals this function is only a very subsidiary one, as at a very early stage a vascular sac-like outgrowth, the **allantois** (Fig. 8), arises from the hinder part of the intestine (*i.e.*, from the splanchnopleure). This serves not only for respiration, but also for the reception of excretory matters derived from the primitive kidney. It is also present in Amphibians, but in them remains small, and does not extend beyond the body cavity of the embryo; while in the Amniota it gradually increases in size and grows round the embryo as a stalked vesicle, which in Reptiles, Birds, and Monotremes comes to lie close beneath the egg-shell and acts as an efficient respiratory organ during the rest of the embryonic period. Towards the close of this period the allantois gradually undergoes more or less complete reduction.

In the higher Mammalia, however, an important vascular connection takes place between the mother and fœtus by means of the allantois. The latter becomes attached to a definite region of the uterine wall, and from it vascular processes or *villi* arise, so that the fœtal and maternal blood-vessels come into very close relations with one another. Thus an **allantoic placenta** is formed, which serves both for the respiration and nutrition of the fœtus (Fig. 9). As an allantoic placenta is not developed in Monotremes and is only slightly indicated amongst Marsupials, these forms are distinguished as **Aplacentalia** from the higher Mammals, or **Placentalia** (p. 14).

The following important points must be noted as regards the structure of the Vertebrate body. After the main organs have appeared, a smaller dorsal **neural tube** and a larger ventral **visceral tube** extend longitudinally through the body, and between the two is a rod-like supporting structure, the **notochord** (p. 5), which arises as an axial thickening of the primary hypoblast and forms the primitive skeletal axis: it is usually replaced by a *vertebral column* consisting of *centra* and *arches*, at a later stage of development (Fig. 7). All these are median in position, and the body is thus
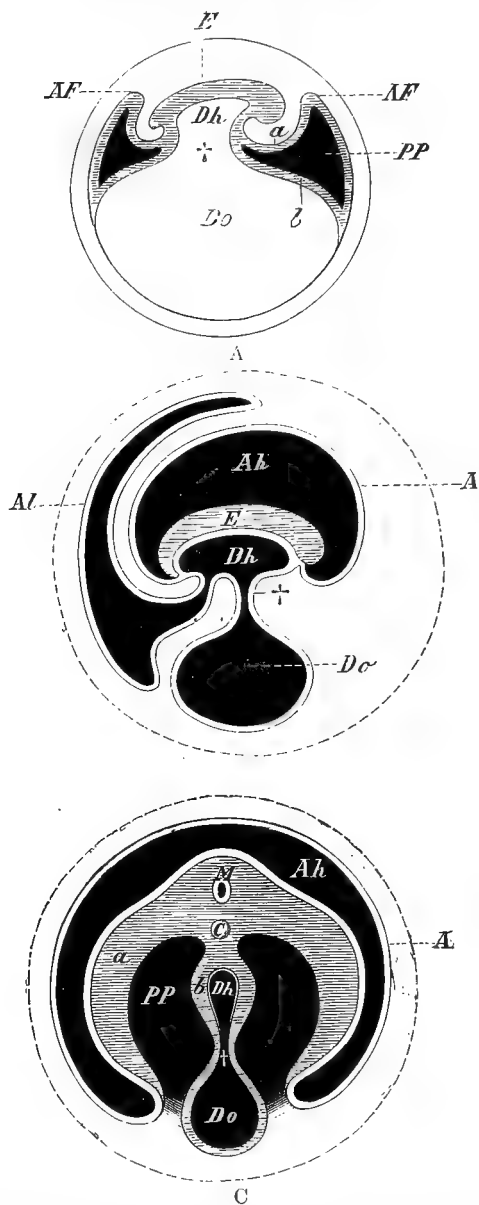
FIG. 8, A, B, AND C.—DIAGRAMS ILLUSTRATING THE FORMATION OF THE AMNION, ALLANTOIS, AND YOLK-SAC. A AND B, IN LONGITUDINAL SECTION ; C, IN TRANSVERSE SECTION.

$E$, embryo ; $Dh$, alimentary cavity ; $Do$, yolk-sac ; †, vitello-intestinal duct ; $PP$, cœlome ; $Ah$, amniotic cavity ; $AF$, amniotic fold ; $A$, amnion ; $Al$, allantois ; $a$, somatopleure ; $b$, splanchnopleure ; $M$, medullary cord ; $C$, notochord.

*bilaterally symmetrical.* The neural tube, or **cerebro-spinal cavity,** enclosed by the *skull* and *vertebral arches,* contains the **central nervous system** (*brain* and *spinal cord*); the visceral tube (*cœlome,* p. 8, Fig. 7) encloses the *viscera* (alimentary canal, urinogenital organs, &c.), and its muscular walls may be strengthened by a series
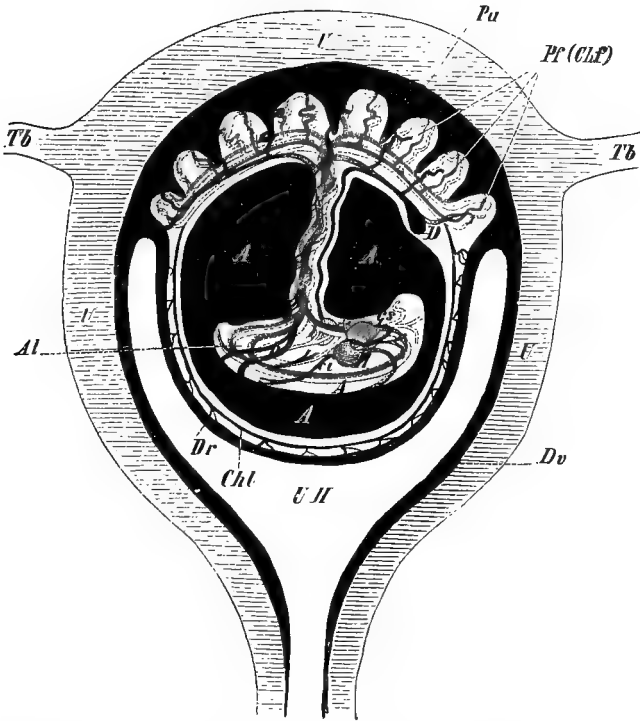


FIG. 9.—DIAGRAMMATIC SECTION THROUGH THE HUMAN GRAVID UTERUS.

*U*, uterus; *Tb, Tb,* Fallopian tubes; *UH,* uterine cavity; *Dv,* decidua vera, which at *Pu* passes into the uterine portion of the placenta; *Dr,* decidua reflexa; *Pf,* fœtal portion of the placenta (chorion frondosum, *Chf*); *Chl,* chorion læve; *A, A,* the cavity of the amnion filled with fluid: in the interior of the amnion is seen the embryo suspended by the twisted umbilical cord; *H,* heart; *A,* aorta; *cs,* precaval, *ci,* postcaval, and *p,* portal vein; *Al,* allantoic (umbilical) arteries; †, the liver, perforated by the umbilical vein; *D,* the remains of the yolk-sac (umbilical vesicle).

of *ribs,* articulating dorsally with the vertebral column. Certain of the ribs may reach the mid-ventral line and come into connection with a *breast-bone* or *sternum,* and thus form complete rings or hoops around the visceral tube.

The anterior ends of the central nervous system (brain) and alimentary tract enter into close relations with the outer world, the

former coming into connection with the higher sense-organs, while from the latter are developed the mechanisms for the taking in of nutriment and for respiration.

The anterior portion of the body, or *head*, passes behind into the *trunk*, either with or without the intermediation of a *neck*. The cœlome is practically restricted to the trunk, in the hinder part of which the intestinal (anal) and urinogenital apertures are situated, and posterior to which again is the *tail*. Head, trunk, and tail constitute the **body-axis**, as distinguished from the *limbs* or **appendages,** which arise from the trunk and of which there are typically two pairs.

## SYSTEMATIC ZOOLOGY.

On the ground of their relationship to one another, animals have been classified into certain divisions and subdivisions, which are designated as *Classes, Orders, Suborders, Families, Genera,* and *Species.*

A general classification of the principal existing Vertebrate groups is given in the following table.

A. **Acrania.**
    Amphioxus (Lancelet).

B. **Craniata.**

I. CYCLOSTOMATA (Suctorial Fishes).
    1. Petromyzontidæ (Lamprey).
    2. Myxinoidæ (Myxine, Bdellostoma).

II. GNATHOSTOMATA (Animals provided with jaws).

    (a.) ANAMNIA (without amnion).
        1. PISCES (True Fishes).
            *a. Elasmobranchii* (Sharks and Rays).
            β. *Holocephali* (Chimæra and Callorhynchus).
            γ. *Ganoidei.*
                1. Selachoidei (*Cartilaginous Ganoids*—Acipenser, Scaphirhynchus, Polyodon).
                2. Teleostoidei (*Bony Ganoids*—Polypterus, Calamoichthys, Lepidosteus, Amia).
            δ. *Teleostei.*
                1. Physostomi (with open pneumatic duct between the air-bladder and pharynx, *e.g.,* Cyprinus, Salmo, Silurus, Mormyrus).
                2. Physoclisti (air-bladder, when present, with closed pneumatic duct, *e.g.,* Perca, Gadus, Lophius, Labrus, Plectognathi, Lophobranchii).

        2. DIPNOI.
            1. Monopneumones (Ceratodus).
            2. Dipneumones (Protopterus, Lepidosiren).

        3. AMPHIBIA.
            *a. Urodela.*
                1. Perennibranchiata (Proteus, Siren, Necturus).
                2. Caducibranchiata.
                    Derotremata (Amphiuma, Menopoma).
                    Myctodera (Salamandra, Triton, Amblystoma).
            β. *Gymnophiona* (Footless Cæcilians).
            γ. *Anura* (Frogs and Toads).

**Ichthyopsida.**

(b. AMNIOTA (Vertebrates which develop an amnion during fœtal life).

1. REPTILIA.
    *a.* *Crocodilia* (Crocodiles and Alligators).
    β. *Lacertilia* (Lizards, including Hatteria).
    γ. *Chelonia* (Turtles and Tortoises).
    δ. *Ophidia* (Snakes).

**Sauropsida.**

2. AVES.
    *a.* *Ratitæ* (Cursorial Birds—Ostrich, Rhea, Emu, &c.).
    β. *Carinatæ* (Birds of flight).

**Mammalia.**

1. *Aplacentalia* or *Achoria*.
    *a.* *Prototheria* or *Ornithodelphia* (Monotremata—Ornithorhynchus and Echidna).
    β. *Metatheria* or *Didelphia* (Marsupialia—Kangaroos, Phalangers, Opossums, &c.).
2. *Placentalia* or *Choriata*.
    *Eutheria* or *Monodelphia*.
        Edentata.
        Sirenia.
        Cetacea.
        Ungulata.
        Hyracoidea.
        Proboscidea.
        Rodentia.
        Cheiroptera.
        Insectivora.
        Carnivora.
        Lemuroidea
        Primates.

TABLE SHOWING THE GRADUAL DEVELOPMENT OF THE VERTEBRATA IN TIME. MODIFIED FROM H. CREDNER.

| | Formation. | Period | Man. | Mammals. | Birds. | Amphibians and Reptiles. | Fishes and Dipnoans. |
|---|---|---|---|---|---|---|---|
| Kainozoic | Recent. | Of the prevalence of warm-blooded animals, particularly Man. | | | | | |
| | Quaternary. Tertiary. | Of the prevalence of Mammals ; the first Man. | | | | | |
| Mesozoic | Cretaceous. Jurassic. Triassic. | Of the maximum development of Reptiles : the first Birds and Mammals. | | | | | |
| Palæozoic | Permian. Carboniferous. | Of the first Amphibians and Reptiles. | | | | | |
| | Devonian. | Of tolerably numerous Fishes (armoured Ganoids). | | | | | |
| | Upper Silurian | Of the first Fishes. | | | | | |
| | Lower Silurian Cambrian. | | | | | | |
| | Archæan. | | | | | | |

# SPECIAL PART.

## A. INTEGUMENT.

THE **skin** consists of a superficial ectodermal and a deeper mesodermal layer. The former is called the **epidermis** (scarf-skin) and the latter the **dermis** (*corium, cutis*). The subcutaneous connective tissue is usually not sharply marked off from the dermis, but the one passes gradually into the other. The epidermis always consists of *cells* only, while the dermis is made up principally of connective tissue *fibres*, and may also enclose muscular fibres. *Bony structures* may occur in the dermis, as well as *vessels* and *glands*, which only rarely extend into the epidermis, from which the glands are all derived and with which they usually remain in connection by means of their *ducts*. *Nerves,* migratory *leucocytes* (lymph- or white blood-corpuscles), *connective-tissue cells*, including *pigment-cells* (*chromatophores*) and *free pigment,* are found in both layers of the integument.

Pigment is never formed in the epithelial or connective-tissue cells themselves, but always originates in the blood.

In the *epidermis* two layers may in general be distinguished :— a superficial, composed of flattened and hardened cells (*stratum corneum, horny layer*), and a deeper layer made up of soft protoplasmic cells (*stratum Malpighii, mucous layer*). The latter serves as a matrix for the regeneration of the horny layer, the superficial part of which is continually scaling off. From the epidermis the *cuticular organs* and *integumentary glands*, and all other parts spoken of as *epidermic structures* take their origin. Such are, hairs, bristles, nails, claws, hoofs, &c. The *peripheral sensory end-organs* of the skin as well as the crystalline lens of the eye also arise by a differentiation of epidermic cells (p. 5): the definite relation which many of these organs have with the dermis must be looked upon as a secondary acquirement.

**Amphioxus, Fishes,** and **Dipnoans.**—The surface of the epidermis is covered with *cilia* in the larval Amphioxus (gastrula stage), and this must undoubtedly be considered as inherited from Invertebrate ancestors. The *striated cuticular border* of the outer

epidermic layer in many fishes (*e.g.* Cyclostomi, Teleostei, and Dipnoi), and, as will be mentioned presently, in Amphibian larvæ, indicates the former possession of cilia (Figs 10 and 11).

•• *Goblet-cells* (*unicellular glands*) are very abundant in the many layered epidermis of Cyclostomes (especially Myxinoids) and osseous Fishes, and are extremely numerous in Protopterus.

Protopterus buries itself in the mud during the dry season, and its integument, which, besides the numerous goblet-cells, also contains simple *multi-cellular glands* like those of the Amphibia, gives rise to a varnish-like secretion as well as to a hardened capsule or " coccoon," by means of which the animal
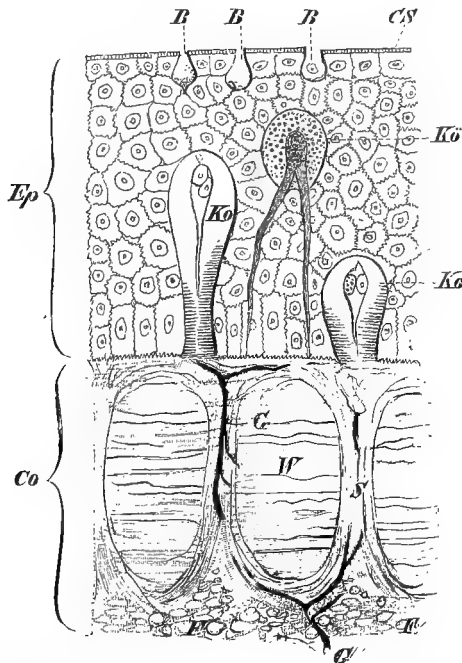


Fig. 10.—Diagrammatic Transverse Section illustrating the Structure of the Skin in Fishes.

*Ep*, epidermis; *Co*, derma; *F*, subcutaneous fat; *CS*, cuticular margin; *Ko*, goblet-cells; *B*, *B*, goblet-cells opening on the surface; *Kö*, granular slime-secreting cells present in Petromyzon and Malopterurus; *G*, vessels which pass upwards in the vertical connective-tissue bundles of the derma; *W*, horizontal connective-tissue bundles.

is protected during its torpid period. In all Fishes which possess slime-secreting cells in the integument, it is probable that the secretion serves to protect the outer skin from the action of the water.

*Multicellular glands* are not commonly present in the integu-

ment of Fishes, but apart from Protopterus (see above) there are a number of exceptions to this rule.

In male Elasmobranchs there is a large *glandula pterygopodii* (gland of the clasper) at the base of each pelvic fin : it arises as a tube-like invagination of the skin, and is in relation with the copulatory organs. Poison-glands are found amongst the Teleostei. Thus in the Weever (Trachinus) there is a series of poison-glands lying on either side of the bases of the spines of the dorsal fin and operculum. In Thalassophryne the operculum is provided with a hollow spine, at the base of which a poison-gland is situated, and in Synanceia there is also a series of glands at the bases of the grooved dorsal spines. Poison organs are also present in Scorpæna and others ; but in many cases in which such organs have been described a more detailed histological examination is desirable. The *phosphorescent* and *eye-like organs* present in the integument of some Fishes (Scopelidæ, Chauliodus, &c.) are probably to be looked upon as modified glands.

In Lepidosiren, apparently in the male only, the integument of the pelvic fins is provided with numerous (? erectile) villi.

*Pigment-cells*, which are under the influence of the nervous system and are able to cause a change of colour, are present sometimes in both layers of the integument, sometimes in the epidermis only. The colouration is sometimes protective (*e.g.* Flat-fishes) and sometimes sexual (*e.g.* Stickleback).

The *bony scales* of Fishes lie in connective-tissue pouches of the dermis and are formed as ossifications of the latter. In Teleosts and Dipnoans they are covered by the epidermis throughout life ; in Ganoids and Elasmobranchs this is only the case in the larva. In Teleosts the parts of the epidermis covering the externally visible portions of the scales become cornified. (For further details compare p. 30).

**Amphibia.**—The epidermis of Amphibian larvæ is for a short period ciliated. In the adult, it may be said in general that the
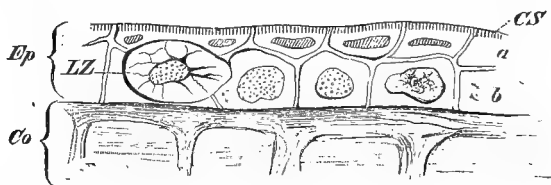


FIG. 11.—SKIN OF LARVA OF SALAMANDER (*Salamandra maculosa*).

*Ep*, epidermis ; *Co*, dermis ; *a*, stratum corneum ; *b*, stratum Malpighii ; *LZ*, Leydig's cells ; *CS*, striated border.

integument of Amphibians is intermediate in structure between that of Fishes and Reptiles.

The epidermis of those larvæ which live in the water consists of two sharply differentiated layers. The outer layer is usually made up of flat cells with a striated cuticular border on their free edge (Fig. 11), like that occurring amongst Fishes : the inner

layer is composed of more cylindrical or cubical cells. The former corresponds to the stratum corneum, the latter to the stratum Malpighii. The horny layer is shed periodically, either entire or in pieces.

Later, with advancing development, the layers of the epidermis become more numerous, and involutions towards the dermis take place in all parts, giving rise to a great number of sac-like and tube-shaped *glands* similar to those of Protopterus (p. 17); these are particularly abundant in certain regions—more especially on the head and flanks (Fig. 12). The individual glands are sur-
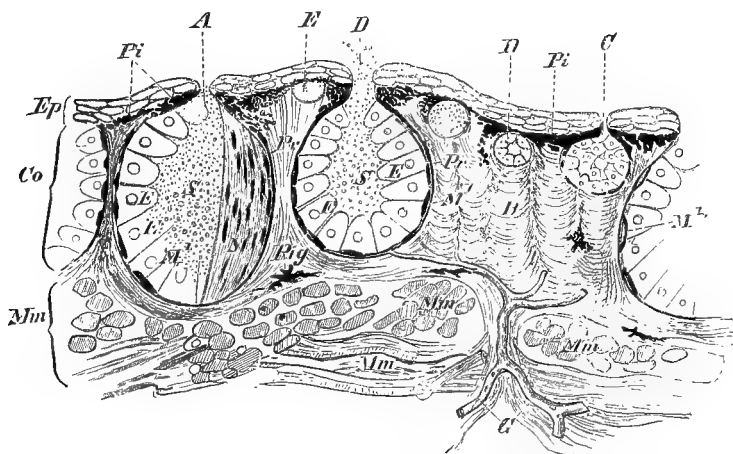


FIG. 12.—SECTION THROUGH THE SKIN OF ADULT SALAMANDER (*S. maculosa*).

*Ep*, epidermis ; *Co*, dermis, in the richly pigmented (*Pi*) connective-tissue stroma of which the various sized integumentary glands (*A*, *C*, *D*, *D*, *E*) lie embedded ; *M¹*, the muscular layer of the glands, lying within the basement membrane (*Pr*) ; *M*, the same, seen from the surface ; *E*, epithelium of glands ; *S*, secretion of glands ; *Mm*, subcutaneous layer of muscles, through which vessels (*G*) extend towards the dermis.

rounded by muscle and connective-tissue fibres, pigment, blood-vessels, and nerves. Their secretion serves to keep the skin moist, but as experiments have shown, it also forms an important weapon of defence on account of its poisonous properties.

This *richness in glands* is a characteristic of the skin of Amphibia and to it they owe their moist and slippery nature. Frequently, as for instance in Toads, the skin is not smooth, but has a rough, warty appearance, caused by local proliferations of the epidermis.

Epidermic *claws*, analogous to those of the Amniota, are present only in Xenopus (Dactylethra) and Onychodactylus.

The *pigment*, accumulated principally in the dermis—partly diffused, partly enclosed within the cells—is under the control of the nervous system, and thus renders a change of colour possible ; and

as the colour becomes modified according to the surroundings of the animal, it may serve as a protection (*e.g.* Hyla).

*Calcifications* may occur in the dermis, or, as in Ceratophrys dorsata, definite *bones* may be formed (see p. 33): the dermis also encloses numerous smooth muscle-fibres.

**Reptilia.**—The characteristic peculiarity of the skin of Reptiles is its capacity of producing *scales* (these are very simple in Geckos and Chameleons), *warts*, *prickles*, *shields* (*e.g.* the "tortoiseshell" of Chelonians), *claws*, *rattles* (Rattlesnake), and other epidermic structures (Fig. 13). All these are due in the first instance to the formation of dermal papillæ, the markedly stratified epidermis covering which becomes cornified *secondarily*. The horny layer of the epidermis may be periodically cast off either entire (Snakes)
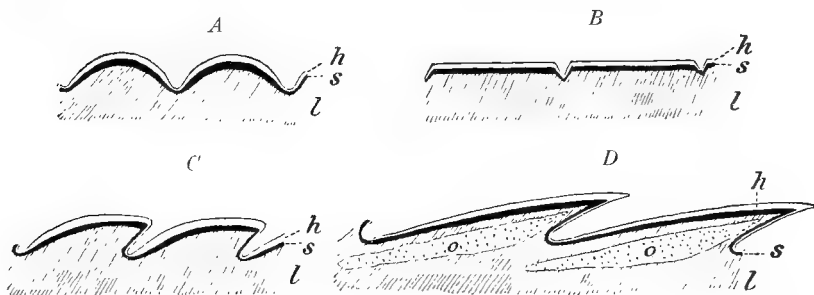


FIG. 13. – DIAGRAMMATIC SECTIONS THROUGH VARIOUS KINDS OF EPIDERMIC SCALES OF REPTILES. (From Boas's *Zoology*.)

*A*, rounded scales ; *B*, shields ; *C*, imbricating scales ; *D*, overlapping scales with bony scutes in the underlying dermis; *h*, horny layer; *s*, Malpighian layer of the epidermis ; *l*, dermis ; *o*, bony scutes.

or in shreds: it is renewed from the Malpighian layer. The integument of Hatteria retains the most primitive characters amongst Reptiles.

*Pigment-cells* occur in the integument, rendering a change of colour possible in many cases (*e.g.* Chameleon).

*Ossifications* in the dermis are very common in Reptiles, and there is great variation in the degree of their development, from the small bony scutes present in Geckos (Ascalabota) to the large exoskeletal plates of Chelonians (see p. 33). Muscles are also present in the dermis. In contrast to the skin of Amphibians, that of Reptiles is entirely wanting in glands.

In Lizards, the so-called *femoral glands* occurring along the ventral side of the thigh are said to be merely solid cones of epidermic cells, which form a series of papillæ or warts and serve as clasping organs during copulation.

**Birds**.—Birds possess a thinner dermis than any other Vertebrates, and it is less plentifully supplied with blood-vessels.

In the deeper layers there is a strongly developed network of muscle-fibres showing traces of transverse striation: these are inserted into the feather-sacs, and serve to erect the feathers.

Apart from a gland present in the neighbourhood of the auditory passage amongst Gallinaceæ, there is only a single gland situated at the base of the rudimentary tail (uropygium): this *uropygial gland* is present in nearly all Birds, and its secretion serves to oil the feathers. Dermal bones are characteristically absent, while epidermic structures, such as *feathers, claws, spurs, foot-scales,* and *beak-sheaths,* are strongly developed.

One of the most marked characteristics of Birds is the possession of *feathers.* In the majority of Birds they are of two kinds—*down-feathers* and *contour-feathers,* and are usually arranged in so-called feather-tracts (*pterylæ*) separated by naked regions (*apteria*). The base of each feather is embedded in an epidermic sac or follicle. Their mode of development corresponds essentially with that of the epidermic scales of Reptiles.

In the region where a feather is to be formed, the dermal tissue becomes raised up towards the ectoderm (Fig. 14, A), and thus gives rise to a vascular papilla. As this papilla grows out to form an elongated cone with a pointed apex, the *feather-germ* (B), its base sinks gradually deeper and deeper into the dermis, and thus becomes surrounded by a sort of pocket—the *feather-follicle.* The horny, as well as the Malpighian layer of the epidermis extends into the base of the follicle, and thence into the feather-germ, the interior of which is throughout filled by cells of the dermis, which give rise to the *pulp.* As the feather-germ keeps on growing, the cells of the Malpighian layer begin to proliferate rapidly, giving rise to a series of radial folds arranged along a central axis, which extend inward towards the pulp, and are immediately bounded by the horny layer (C). These folds, between which the nutritive pulp extends, then become cornified and separated from above downwards from the surrounding cells ; and, by a gradual drying of the central pulp-substance, give rise to a tuft of horny rays, which are, however, at first bound together by the enclosing stratum corneum. Most Birds are hatched when the feathers are in this stage of development, and they thus appear as if covered with brush-like hairs.

By the shedding of the surrounding horny layer the rays or *barbs* become free (D), and if these are all similar to one another, an embryonic *down-feather* is formed. The whole feather-germ, however, does not become divided up into barbs in this manner : its lower portion, embedded in the skin, retains a more uniform character and forms the *quill (calamus).*

The embryonic down-feathers (E), on the individual barbs of which smaller secondary rays or *barbules* become developed, may retain their character as such throughout life or may be replaced by definitive feathers. In this case a second, larger, follicle early arises from the base of the follicle of the down-feather, the pulp of the two being in connection (D). The papilla developing within the interior of this new follicle grows rapidly, gradually pushes the base of the down-feather out of its follicle, and comes to the surface.

Each contour feather (*penna*) at first closely resembles a down-feather (*pluma*) in structure, and consists of a tuft of similar rays or *barbs* provided with secondary rays or *barbules.* In the course of further growth, however, one of the rays becomes rapidly

thickened, and forms a main axis or *stem (scapus)*, to which the barbs are attached on either side. The proximal or basal portion of the scapus which bears no barbs is called the *quill (calamus)*, and the distal part, to which the barbs are attached, the *shaft (rachis)*. The barbs together constitute the *vane (vexillum)* (Fig. 14, F).
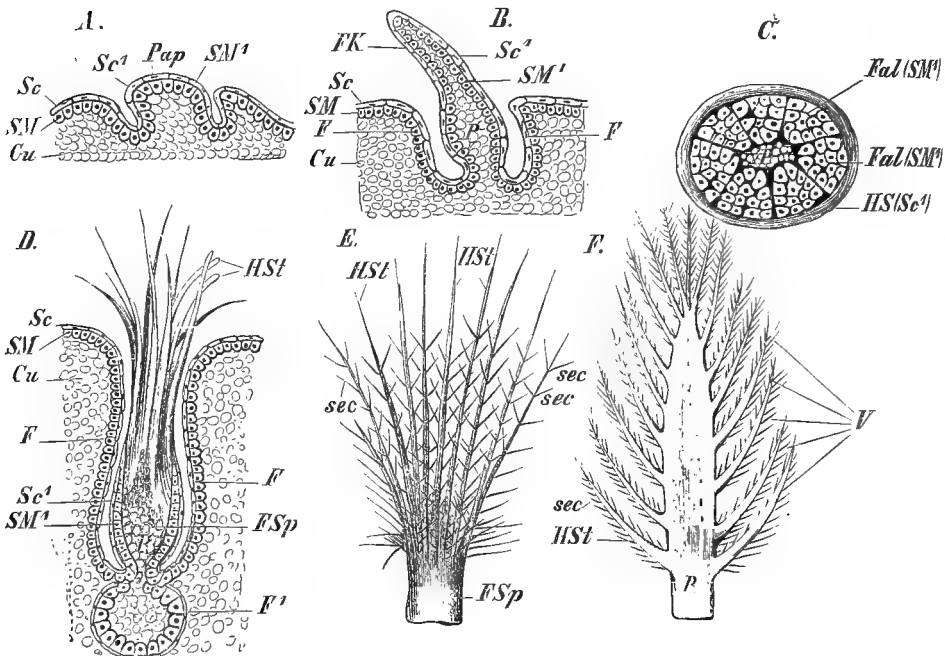


FIG. 14. —SIX STAGES IN THE DEVELOPMENT OF THE FEATHER.
(Mainly after Th. Studer.)

*Cu*, dermis ; *SM*, stratum Malpighii ; *Sc*, stratum corneum ; $SM^1$, $Sc^1$, extensions of these tissues into the feather-papilla, *Pap*; *FK*, feather-germ ; *F*, $F^1$, feather-follicle ; *P*, pulp ; *Fal* ($SM^1$), folds of the Malpighian layer extending into the feather-germ, and enclosed externally by the horny layer, *HS* ($Sc^1$) : both layers are seen in the transverse section (C); *FSp*, quill of feather, which breaks up above into a tuft of rays or barbs (*HSt*) ; *sec, sec*, secondary rays (barbules) arising from the latter ; *R*, rachis ; *V*, vexillum. For further details as to the different stages A-F, compare text.

The barbules are so arranged on each barb as to make the latter resemble an entire feather in appearance. The barbs may become very closely united together by means of minute hooks on the barbules, so that an extremely strong and resistant though pliant structure is formed; this is especially the case in the large wing and tail feathers (*remiges* and *rectrices*).

In many Birds each quill of the ordinary feathers of the body bears two vexilla, the second being spoken of as the *aftershaft (hyporachis)*.

A periodic casting of feathers, or *moulting*, takes place in all Birds, and corresponds to the similar process of the casting of the horny layer of the skin in Amphibians and Reptiles.

The feather-covering of Birds must have been acquired in very early geological periods, for Archæopteryx, found in the Jurassic strata of Bavaria, possessed well-formed feathers with a very delicate shaft and vane. Palæonto-logical researches have not brought to light any definite intermediate stages between scales and feathers, but that they must once have existed is shown by the development of these structures.

**Mammals.**—The integument of Mammals gives rise to *hairs*, which are characteristic of and confined to this Class. They may be almost uniformly developed all over the body and even on the soles of the feet, or may become reduced in more or less extensive regions. They are most scanty in the Cetacea, where only a few occur on the lips, and even these may disappear in the adult. The first to appear are certain *tactile-hairs* (*vibrissæ*) on the head, along the course of the trigeminal nerve; all the hairs, however, serve as tactile organs as well as for keeping the body warm.

Nothing definite can be at present stated as regards the phylogeny of hairs, but it seems at any rate probable that they are not directly comparable to the scales of Reptiles and feathers of Birds:[1] the arrangement of the hairs in alternating groups is probably the last indication of the former possession of scales.

Each hair first arises as a proliferation of the epidermic cells in the region of the Malpighian layer which comes to project inwards towards the dermis (Fig. 15, A, B and C). In this manner the *hair-germ* is formed. Thus the epidermic portion is the *primary* one; a corresponding dermal papilla is formed *secondarily*, and is the homologue of the papilla which forms the first trace of the scale in a Reptile or the feather in a Bird.

The thickening of the epidermis then grows downwards in the form of a papilla and becomes surrounded by the cells of the dermis, so that, as in the case of the feather, it comes to lie within a kind of pocket, the *hair-follicle* (Fig. 14, C). The originally uniform mass of cells of the hair-germ later becomes differentiated into a peripheral and a central portion. The latter consists of more elongated cells, and gives rise later to the *hair-shaft* with its *medulla* or *pith*, and to the *cortex*, as well as to the *cuticle* of the shaft and the so-called *inner root-sheath*; the former gives rise the *outer root-sheath* (comp. Fig. 16 A, which represents the fully-formed hair). The base of the hair-shaft which fills up the bottom of the follicle is broadened out to form the *hair-bulb* (Fig. 15, D), which grows round the later formed and highly vascular hair-papilla like a cap (C, D). At *Dr*, in D, the *sebaceous glands* (p. 27) are seen arising by a proliferation of the Malpighian cells. The hair usually breaks through the skin in an oblique direction; the direction differing in different parts of the body.

The hair or *hair-shaft* embedded at its base in the *hair-follicle*, is more or less cylindrical: it consists of three parts—

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[1] It has been suggested that the hairs correspond to modified integumentary sense-organs such as occur in the lower Vertebrates (comp. Figs. 15 and 150).

*medulla*, *cortex*, and *cuticle* (Fig. 16 A), all of which are formed from cells. The follicular tissue, which is richly provided with blood-vessels, extends into the bulb-like base or root of the hair-
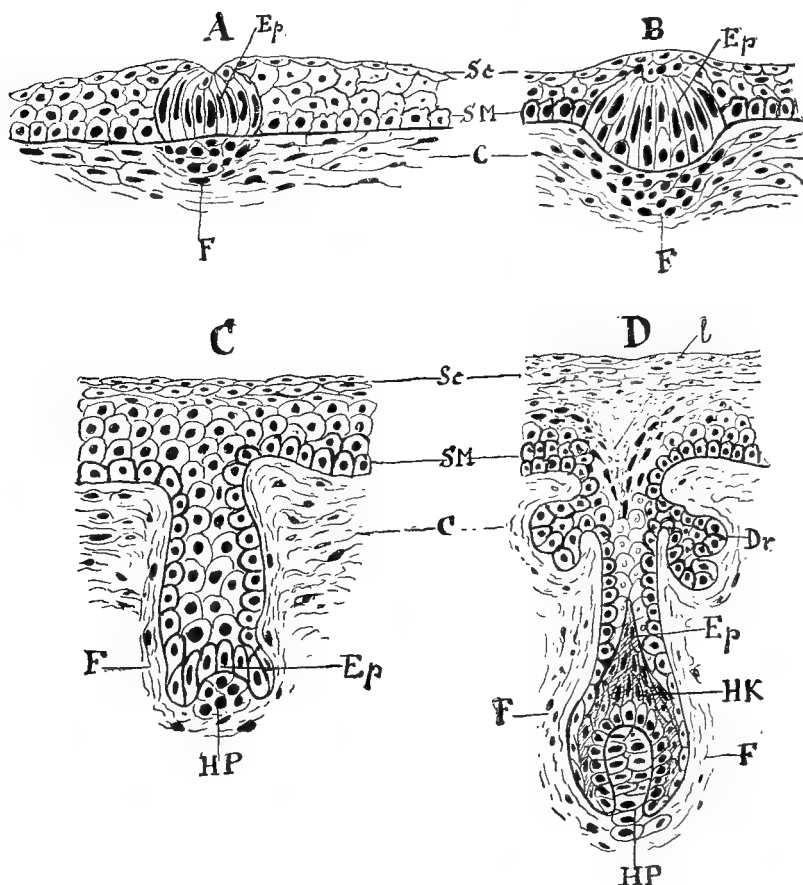


FIG. 15.—DIAGRAMS OF FOUR STAGES (A-D) IN THE DEVELOPMENT OF HAIRS. (After F. Maurer.)

*Sc*, stratum corneum; *SM*, stratum Malpighii, which gives rise to an epithelial knob at *Ep*; this grows inwards into the dermis (C); *F*, rudiment of the hair-follicle; *HP*, hair-papilla; *HK*, hair-bulb; *Dr*, rudiment of the sebaceous gland. In D, *l* indicates the stratum lucidum with eleidin-granules in the cells.

shaft, and gives rise to the *hair-papilla*. From this region a new hair-shaft may develop when the hair is shed, periodically or non-periodically as the case may be, often by the formation of a new papilla. The colour of the hair is due to three causes :—Firstly,

to the greater or less accumulation of pigment in the cells of the
cortical layer; secondly, to the air contained in the intercellular
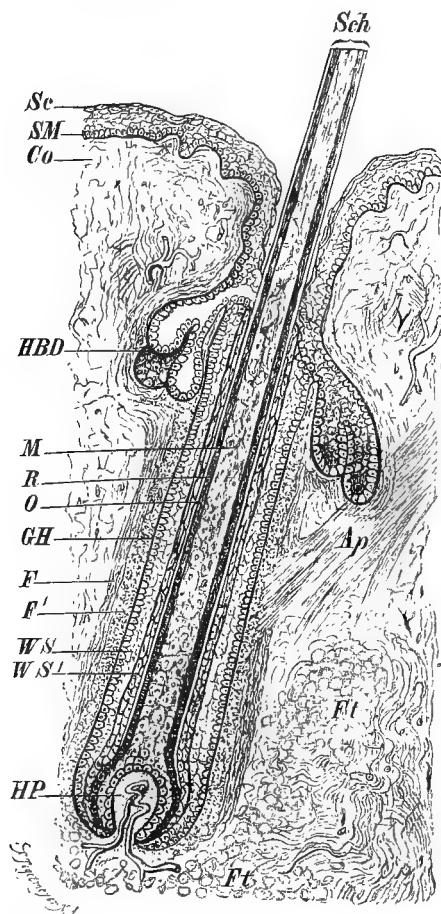


Fig. 16, A.—Longitudinal Section through a Hair. (Diagrammatic.)

*Sc*, stratum corneum; *SM*, stratum Malpighii; *Co*, dermis; *Ap*, arrectores pili;
*Ft*, adipose tissue; *F*, outer longitudinal layer, and *F¹*, inner transverse layer
of dermic coat (both composed of connective-tissue); *Sch*, hair-shaft; *M*,
medulla; *R*, cortex; *O*, cuticle of shaft; *WS*, *WS¹*, external and internal
root-sheath,—the latter reaches above only as far as the point of entrance of
the ducts of the sebaceous glands (*HBD*); *HP*, hair-papilla, containing
vessels; *GH*, hyaline layer, which lies between the inner and outer hair-
sheaths, *i.e.*, between the root-sheath and the follicle (dermic coat).

spaces of the medulla; and lastly, to the nature of the surface of
the hair, *i.e.*, whether it is rough or smooth. The hairs are usually
arranged in groups of finer and coarser elements, and, especially
in the case of the vibrissæ, are well innervated.

A richer hairy covering (*lanugo*) is often met with in the embryonic -condition—as, for instance, in the human fœtus—than occurs later; and this fact, together with the occasional appearance of abnormally hairy individuals, indicates that at one time Man was distinguished by a far more abundant clothing of hair than at the present day.

Other epidermic structures, formed as thickenings of the horny layer, also play a very important part in Mammals; such are— *claws, nails, bristles,* and *spines* (Hedgehog, Porcupine); the so-called whalebone (*baleen*) of the Mystaceti; the *horn-sheaths* in Ruminants; the *nasal horns* of the Rhinoceros; the *scales* in Manis and on the tail of the Beaver and other Mammals; the *palatal plates* of Sirenia; and the *ischial callosities* of certain Apes.

When *pigment* is present, as, for instance, on the snout in many Mammals and on the external genitals (labia majora and scrotum) and the teats in the human subject, it is always situated in cells of the Malpighian layer.

The outer layer of the dermis, as may be seen by a glance at Fig. 16, B, may be divided into an outer papillary and an inner reticular portion. The papillæ of the former are accurately adapted to the over-lying epidermis: some of them contain blood- and lymph-capillaries, and others, nerves with tactile corpuscles. The latter, on the other hand, becomes lost without any sharp boundary line in the sub-dermal connective-tissue and in the more or less strongly-developed fatty layer (panniculus adiposus). The pads (*tori*) on the soles of the feet of most Mammals are due to large dermal papillæ.



FIG. 16, B.—SECTION THROUGH THE HUMAN SKIN.

*Sc*, stratum corneum; *SM*, stratum Malpighii; *Co*, dermis; *F, F*, subcutaneous fat; *NP*, sensory papillæ; *GP*, vascular papillæ; *N* and *G*, nerves and vessels of the dermis; *SD, SD*, sweat-glands, with their ducts (*SD¹, SD¹*); *H*, hair with sebaceous glands (*D*).

In addition to numerous elastic fibres, smooth muscle elements are distributed throughout the dermis; they are particularly abundant in the scrotum (*dartos*) and in the teats, and are present in connection with the hair-sacs (*arrectores pili*): the power of erecting the hair possessed by many Mammals is due to these (Fig. 16, A). A bony *dermal skeleton* is found only in the Armadillo amongst existing Mammals (comp. p. 34).

The integumentary glands, which are well developed in all Mammals except the Cetacea, are of two kinds, *tubular* and *acinous*. The former include the *sweat-glands* and their various modifications; while the latter are spoken of as *sebaceous glands*, and include the already-mentioned *glands of the hair-sacs*, which serve to oil the hair (Figs. 15 D, and 16, A and B), the *preputial glands*, the *inguinal glands* of certain Rodents, the *Meibomian glands* of the eyelids, and many others. It must be borne in mind, however, that there is not always a sharp distinction between these two kinds of glands.

The paired *femoral gland* of Ornithorhynchus opens by means of a long duct on to the spur present on the hind foot. Its secretion is poisonous.

Another important modification of the integumentary glands of the Mammalia is seen in the *mammary glands*, which secrete
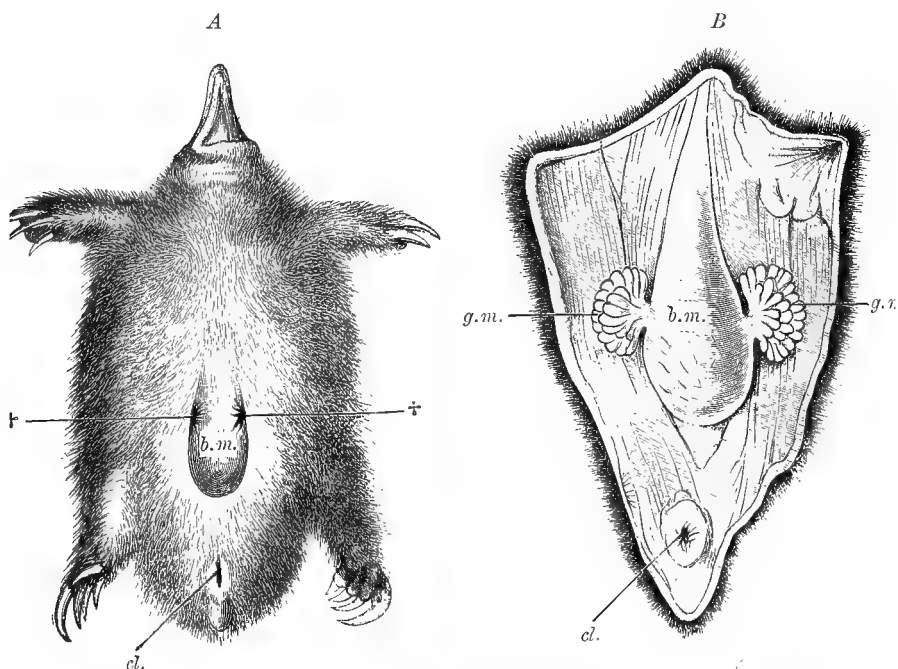


FIG. 17, A.—*A*, VENTRAL VIEW OF A BROODING FEMALE OF *Echidna hystrix*. *B*, DISSECTION OF THE VENTRAL INTEGUMENT FROM THE DORSAL (INNER) SIDE. (After W. Haacke.)

†, ·†, the two tufts of hair in the lateral folds of the mammary pouch (*b.m.*) from which the secretion flows. On either side of the pouch, which is surrounded by strong muscles, a group of mammary glands (*g.m.*) opens; *cl*, cloaca.

milk for the nutrition of the young. In Monotremes these apparently correspond to sweat glands, while in other Mammals they represent sebaceous glands.

Monotremes possess no *teats*, and the milk probably passes along the hairs, which in this region are arranged in bunches, and is then licked off by the young animal. The gland is compressed by a strong sphincter muscle. In Echidna, a *mammary* or *marsupial pouch* which is primarily paired and becomes unpaired secondarily, is early formed for the reception of the young, and the gland-masses open into two depressions of the ventral integument where the bunches of hair are situated (Fig. 17). These depressions may be called *mammary pockets*, and are of especial interest as they represent the first stage in the development of the various forms of teats present in all other Mammalia, in many of which distinct indications of the Monotreme condition are met with. The marsupial pouch of the Marsupialia is probably homologus with that of Echidna.

Thus a similar mammary pocket is formed in the embryos of Marsupials and placental Mammals by the epidermis extending inwards towards the dermis, and cylindrical, more or less branched processes arising from the base of the pocket thus formed (Fig. 17, B, *A*). These processes only are the glands proper, the mammary pocket being simply a part of the outer surface of the skin which has sunk inwards, and thus it may give rise to hairs and other integumentary structures.

The teats may become developed in one of two ways. In the first of these, the skin surrounding the pouch becomes raised up to form a circular rampart, and thus gives rise to a teat perforated by a canal, into the base of which the ducts of the gland open (Fig. 17, B, *B*). In the second case, the gland surface itself becomes elevated into a papilla, while the surrounding
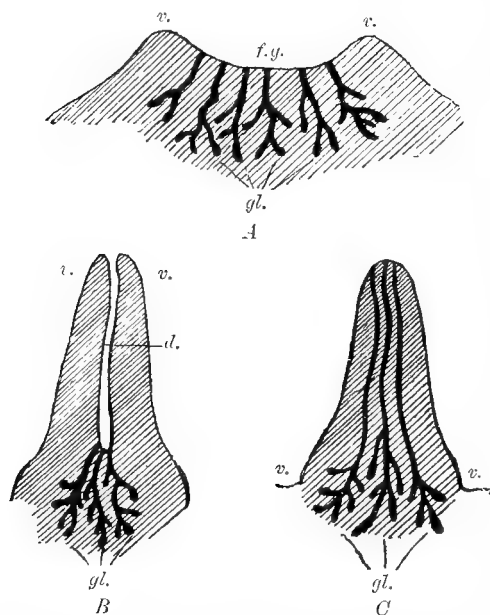


Fig. 17, B.—Diagrammatic Representations of the Early Development of the Leading Types of Mammary Glands. (Modified from Gegenbaur.)

*A*, first or undifferentiated (mammary pit) stage ; *B*, stage of the false teat ; *C*, stage of the true teat ; *r*, *r*, rim (or rampart) of the glandular area ; *f*, *g*, glandular area ; *gl*, mammary glands ; *d*, mammary canal.

skin remains almost on a level with the rest of the integument (*C*). In the latter case the teats may be described as *true* or *secondary* (Marsupials, Rodents, Lemurs, Monkeys, and Man), and in the former as *pseudo-* or *primary* teats (Carnivora, Pigs, Horses, and Ruminants). The latter condition is already indicated in certain Marsupials (*e.g.* Phalangista vulpina).

The number of teats varies greatly : there may be as few as one pair, or as many as eleven pairs (Centetes). They are often situated in two nearly parallel rows along the ventral side of the thorax and abdomen which slightly converge towards the inguinal region : in other cases they may be restricted either to the inguinal (Ungulates and Cetaceans) or to the thoracic region (Sloths, Elephants, Sirenia, many Lemurs, Cheiroptera, and Primates) : while in others, they may be axillary or abdominal, or they may occur in various combinations of all these regions.

In the male, the mammary apparatus becomes aborted, though usually at birth and puberty milk is produced in the human subject. Male goats and castrated sheep have also been known to give milk, and the same is probably true of male Bats. The occasional existence in men of supernumerary teats, and in women of supernumerary mammæ and teats (*polymastism* and *polythelism*) is very remarkable. They are usually situated in the thoracic region, and must be considered as atavistic to a primitive form which possessed numerous teats and which produced a number of young at a time. Such a transition from polymastism to bimastism may be seen plainly at the present day in the Lemurs : in them the inguinal and abdominal teats are seen in various degrees of retrogressive metamorphosis, while a single pair of thoracic teats remain well developed. This accords with the fact that most Lemurs bear only a pair of young ones at a time, which they carry with them at the breast. Moreover, in various Mammals a greater number of teats are present in the embryo than in the adult.

The mammary glands, which are at first solid, become secondarily hollowed out and further differentiated. The whole intermediate tissue during lactation is filled with white blood-corpuscles (leucocytes); and possibly the well-known structural elements of milk, known as colostrums and milk-spheres, owe their origin to these corpuscles, which have passed through the walls of the acini.

## B. SKELETON.

## 1. EXOSKELETON.

THE hard exoskeleton, consisting of *bone* or other *calcified tissues*, must be distinguished from the horny exoskeletal parts described in the last chapter, in which, however, the former was also referred to. Thus it will be remembered that the term " scale " is sometimes used for a horny epidermal structure, and sometimes for a bony dermal one (pp. 18, 20).

The first and most primitive hard structures in Vertebrates are met with amongst **Elasmobranchs** in the form of small, pointed denticles (*placoid organs*) in the skin ; these consist of *enamel* and *dentine*, resting on a basal plate of *bone*, thus resembling in structure ordinary oral teeth, which will be described later. Primitively, as in many Rays, there is a relatively small number of these placoids, which do not touch one another, while in most Sharks and Dogfishes they are much more numerous and close-set (Fig. 18). Their shape is rhombic or more or less rounded, each bearing a spine, and new ones being continually formed. The enamel, developed in connection with epidermic cells, is the *primary* part of the denticle (Fig. 19) ; the dentine is developed *secondarily*—that is, later—from the phyletically younger mesoderm, and this is also true of the bony portion. The enamel is therefore the first, and originally the only hard substance of the placoid organ.

The first bony tissue to be developed is thus formed in connection with



FIG. 18.—DERMAL DENTICLES OF *Centrophorus calceus.* (Slightly magnified.) (From Gegenbaur's *Comp. Anatomy.*)

these denticles, the basal-plate representing an accessory portion
of the denticle, and serving to fix it within the skin. In the
further course of evolution the denticle itself undergoes reduc-
tion, the basal-plate remaining as an independent structure.
This is illustrated by a study of the exoskeleton in other
Vertebrates.

In the **Holocephali** dermal denticles are only present on
certain appendages (the claspers), and the first dorsal-fin is
strengthened by a large bony spine.

In most **Ganoids** thick plates, usually rhombic in form, are
present in the skin ; in bony Ganoids these cover the entire
body, their margins being in apposition.[1] These *ganoid-scales*
correspond to the main (deeper) part of the placoid basal-plates,.
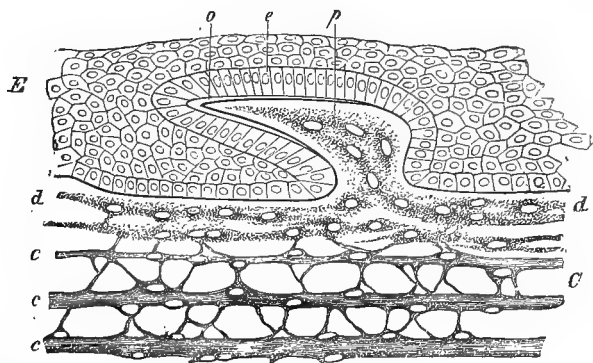


Fig. 19.—Vertical Section through the Skin of an Embryo Shark.
(From Gegenbaur's *Comp. Anatomy.*)

C, dermis ; c, c, c, d, layers of the dermis ; p, papilla ; E, epidermis ; e, its layer
of columnar cells ; o, enamel layer.

the spine having become rudimentary. Their surface is dense
and smooth (*ganoin-layer*), and was formerly erroneously supposed
to consist of enamel. In Lepidosteus they bear numerous small
denticles ; but from what has been said above, this fact does
not indicate that each ganoid-scale corresponds to a multiple
of placoids. The exoskeleton was largely developed amongst fossil
Ganoids.

The scales of **Teleosts,** the first indication of which, as in
the case of placoid scales, is seen in the form of small papillæ of
the dermis extending into the epidermis, correspond to the super-
ficial portions of the basal-plates. In the further course of develop-
ment they are seen to consist of bony plates arranged in oblique
rows and lying directly beneath the epidermis, the individual scales
not touching one another, and their surfaces lying parallel to the

[1] In Amia, the scales have a " cycloid " form. (See note on p. 32.)

surface of the body. In this stage their arrangement resembles that seen in Ganoids. Subsequently they usually come to lie within definite pockets or sacs, and to overlap one another like tiles on a roof (Fig. 20 A). The surface of the scales may be sculptured.[1]
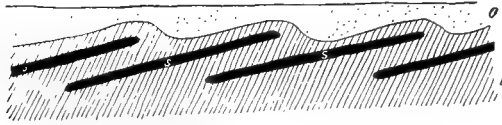


FIG. 20A.—DIAGRAMMATIC LONGITUDINAL SECTION THROUGH THE SKIN OF A TELEOSTEAN, TO SHOW THE RELATION OF THE BONY SCALES. (From Boas's *Zoology*.)

*l*, dermis ; *s*, scale ; *o*, epidermis.

Amongst the Siluridæ (Fig. 20, B), Plectognathi, and Lophobranchii, they may be of relatively large size and so arranged as to form a strong bony cuirass.

Scales are wanting in Cyclostomes, and may be reduced or absent in representatives of the three larger Orders described above (*viz.*, in Electric Fishes Spatularia, and some Eels).

In the **Dipnoi** the arrangement of the scales is similar to that seen in the Teleostei. They consist of an external hard substance
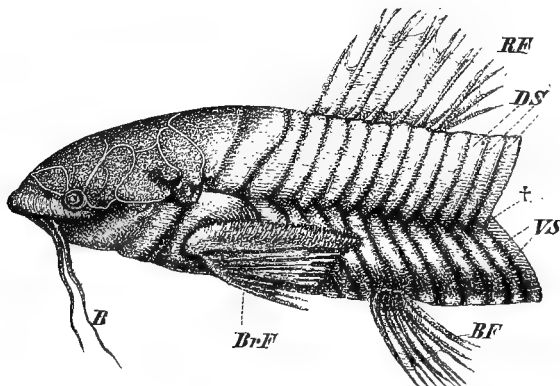


FIG. 20B.—DERMAL ARMATURE OF *Callichthys*.

*B*, barbules ; *BrF*, pectoral fin ; *BF*, pelvic fin ; *RF*, dorsal fin ; *DS* and *VS*, dorsal and ventral bony shields ; †, lateral line.

arranged in a network and provided with numerous denticles, and of an internal portion composed of firm connective-tissue and bone.

[1] Different forms of the rounded or polygonal scales in Teleostei are distinguished as *cycloid* and *ctenoid*. The former, which are the more primitive, have a smooth margin, while in the latter the posterior margin is toothed and comb-like. Various intermediate stages exist between the two forms.

These denticles are developed from connective-tissue cells, and are not comparable to the placoid denticle; the resemblance, too, between the scales of the Dipnoi and Teleostei is only a superficial one.

Thus the exoskeleton plays an important part in Fishes, and in numerous fossil **Amphibians** it reached a still higher development (Stegocephala). Amongst these, specially strong dermal plates were formed in the region of the shoulder-girdle, and very commonly most of the body was covered with scales. Fossil genera of Amphibia have, however, bequeathed but slight traces of this strong dermal armour to the existing forms of the group: as examples may be mentioned the bony plates in the skin of the back of certain Anura (Ceratophrys dorsata and Ephippifer aurantiacus), as well as the scales lying between the ring-like scutes of
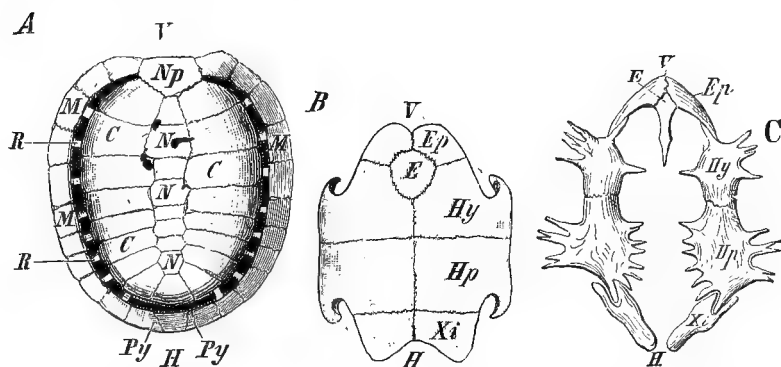


FIG. 21.—A, CARAPACE, and B, PLASTRON OF A YOUNG TESTUDO GRÆCA; C, PLASTRON OF CHELONE MIDAS.

*NN*, neural plates; *C, C*, costal plates; *MM*, marginal plates; *Np*, nuchal plate; *Py, Py*, pygal plates; *E*, entoplastron; *Ep*, epiplastron; *Hy*, hyoplastron; *Hp*, hypoplastron; *Xi*, xiphiplastron; *R, R*, ribs. (*V* indicates the anterior, and *H* the posterior end.)

the footless Amphibia (Gymnophiona). The latter resemble in many points the scales of Fishes and Dipnoans, and may be derived from such a scaly covering as that of the Permian Salamander, Discosaurus.

The dermal skeleton was still more highly developed amongst fossil **Reptiles,** *e.g.*, many Ornithoscelida (Stegosaurus). In these, enormous bony plates and spines, sometimes as much as sixty-three centimetres long, were present in the dorsal region. Teleosaurus also, as well as the Triassic Aëtosaurus ferratus and the Cretaceous Nodosaurus textilis, possessed a strong exoskeleton. Amongst existing Reptiles (comp. p. 20), Crocodiles, many Lizards (Anguis, Cyclodus, Scincus), and more especially Chelonians, exhibit a well-developed dermal skeleton. In the latter Order

there is a dorsal and a ventral shield (*carapace* and *plastron*) consisting of numerous pieces and completely enclosing the body (Fig. 21). Both arise independently of the endoskeleton, which is preformed in cartilage : that is to say, they are true exoskeletal membrane bones (cp. note on p. 71). The exoskeleton, however, comes into the closest relation with the endoskeleton, and may supplant it here and there : thus, in Testudo, for instance, the thoracic and lumbar vertebræ and ribs become quite rudimentary.

**Birds,** as already mentioned in the chapter on the integument, have no dermal skeleton, and this is true of all **Mammals** except Armadillos (Dasypodidæ). In these it consists of a series of movable transverse bony scutes covering the head and body and of smaller plates on the tail and limbs. Sparse hairs occur between these plates. It is very doubtful whether this exoskeleton has been derived from that of Reptiles : more probably it, like the horny exoskeleton of Manis (p. 26), has arisen secondarily, and in consequence of its development the hairs have become reduced. In Glyptodon, a fossil member of this group, the dermal plates were firmly united together to form a large shield which covered the whole body.

## 2. ENDOSKELETON.

### I. VERTEBRAL COLUMN.

An elastic rod, the **notochord** or **chorda dorsalis,** lying in the longitudinal axis of the embryo between the neural and visceral tubes (see p. 9), is the first part of the endoskeleton to be formed, and is the fore-runner of the vertebral column. It is developed as a ridge of the primitive hypoblast, from which it becomes constricted off, and is therefore of epithelial origin. The large parenchyma-like cells of which it is composed consequently do not give rise to any intercellular substance ; vacuoles, however, soon appear within the cells, the protoplasm of which undergoes modification, and thus a retrogressive metamorphosis sets in (Fig. 22). The fact that this occurs at such early stages of development shows that the notochord must long ago have begun to lose its primitive function, whatever that function may have been.

As these degenerative processes are gradually carried still further, only the walls of the cells persist in the greater part of the notochord ; these become flattened by mutual pressure, so that they appear like a meshwork of pith-cells. At the periphery, however, the cells retain their protoplasm, and become arranged like an epithelium. Around the notochord two *sheaths* (Fig. 22 *A, B*)
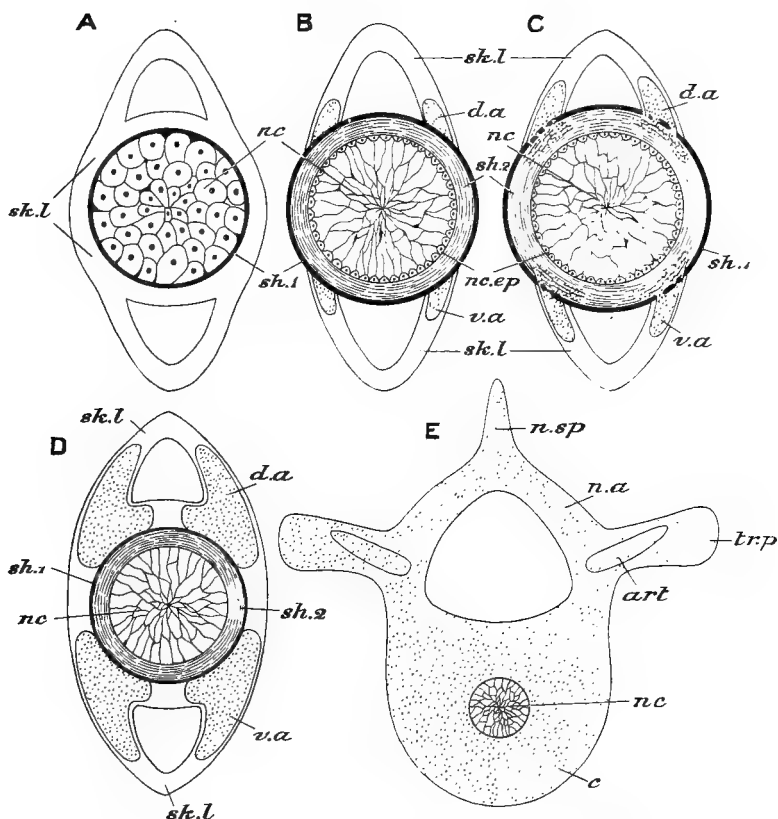
FIG. 22.—DIAGRAMS ILLUSTRATING THE DEVELOPMENT OF THE NOTOCHORDAL
SHEATHS AND VERTEBRAL COLUMN.

*A.*—Early stage, showing notochordal cells (*nc*) and primary sheath (*sh*[1]), as well
as the mesoblastic skeletogenous layer (*sk.l*).

*B.*—Later stage, in which the central notochordal cells (*nc*) have become
vacuolated and the peripheral cells have given rise to the " notochordal epithe-
lium" (*nc. ep.*) from which the fibrillar secondary sheath (*sh*[2]) is derived :
paired dorsal and ventral cartilages (*d.a, v.a*) have arisen in the skeletogenous
layer.

*C.*—Cartilage cells have passed through the primary sheath, and are invading
the secondary sheath (Cartilaginous Ganoids, Holocephali, Dipnoi, Elasmo-
branchii : in the last named *chorda-centra* are thus formed).

*D.*—The cartilages are growing round the notochord, outside its sheaths, which
gradually become reduced : thus *arch-centra* are formed (Bony Ganoids,
Teleostei, Amphibia, Amniota).

*A —D* represent the caudal region.

*E.*—A later stage in the development of a pre-caudal vertebra. The notochord
(*nc*) has become constricted, and the cartilages have united into a single mass
and have given rise to a centrum (*c*), neural arch (*n.a*), neural spine (*n. sp*),
transverse processes (*tr.p*) and articular processes (*art*):

are successively developed from its cells, and these differ both chemically and physically from one another. The *primary sheath* (so-called *elastica*) is first secreted by the peripheral notochordal cells: the *secondary sheath*, which has a similar origin from the so-called "notochordal epithelium," appears later, and occurs in all the Craniata; it is said not to be present in Amphioxus, the notochord of which, like that of the Tunicata, apparently represents the oldest and most primitive form of this structure, such as is still repeated ontogenetically in Elasmobranchs. The thick secondary sheath, which like the primary, is at first homogeneous, gradually becomes fibrillar and replaces the primary sheath functionally.

From the surrounding mesoblast a *skeletogenous layer* is developed: this not only surrounds the notochord, but extends dorsally to it as well as ventrally (Fig. 22). Thus a continuous tube of embryonic connective-tissue is formed enclosing the spinal cord and only broken through at the points of exit of the spinal nerves. This stage is known as the *membranous stage*, and in it no indication is seen of the segmentation which occurs later in the vertebral axis. The cause of this segmentation is to be traced primarily to the muscular-system; and it is evident, for mechanical reasons, that the segmentation of the vertebral column must alternate with that of the muscular segments or myotomes. Small masses of cartilage arranged metamerically later appear in the skeletogenous tissue close to the notochord, and these represent the rudiments of the dorsal and ventral *arches* and *bodies* or *centra* of the *vertebræ* (Fig. 22, B, D, E). This is the beginning of the second or *cartilaginous stage* of the vertebral column; the various *processes* (spinous, transverse, articular, &c., Fig. 22, E) are then formed, and now ossification may occur (*bony stage*). Those parts of the fibrous tissue which do not become consolidated in this manner give rise to the *ligaments* of the vertebral column.

During these differentiations of the skeletogenous tissue, the notochord suffers a very different fate in the various Vertebrate groups; it may increase in size and persist as a regular cylindrical rod, or it may become constricted at definite intervals by the formation of vertebral bodies, or even entirely disappear.

All these ontogenetic stages find their exact parallel in the phylogenetic development of Vertebrates, as the following pages will show.

**Amphioxus,** as already mentioned, apparently possesses the most embryonic type of notochord. It is surrounded by a connective-tissue layer and is entirely unsegmented.

In **Cyclostomes** a very similar primitive condition is retained; but a secondary sheath becomes developed, and cartilaginous elements appear in the caudal region: in the adult Petromyzon these are present all along the notochord in the form of rudi-

mentary *neural* (*dorsal*) *arches*, which, however, do not meet above the spinal cord. These cartilages, of which there are two pairs to each muscular segment or myotome, correspond to the "intercalary pieces" of Elasmobranchs (p. 38); they serve in the first instance for the origin and insertion of the muscles, and at the same time form a protection for the spinal cord. *Neural spines* also occur in the middle of the axis, and in the caudal region *hæmal* (*ventral*) *arches* enclosing the caudal aorta and vein, as well as *hæmal spines*, are present, and fusion of the cartilaginous elements occurs.

To the condition found in Cyclostomes, that seen in the **Cartilaginous Ganoids, Holocephali,** and **Dipnoi** is directly connected, inasmuch as the metameric character of the skeletal axis
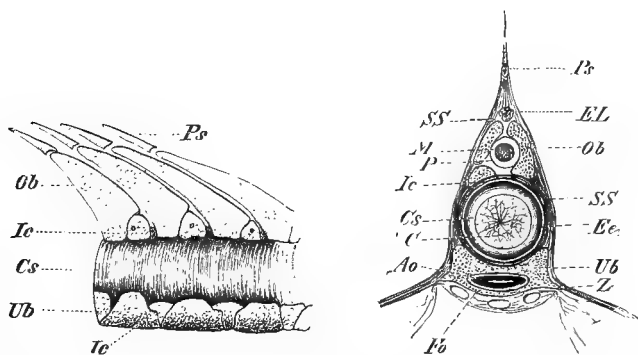


FIG. 23.—PORTION OF THE VERTEBRAL COLUMN OF *Spatularia*. (Side view.)

FIG. 24.—TRANSVERSE SECTION OF THE VERTEBRAL COLUMN OF *Acipenser ruthenus* (in the anterior part of the body).

*Ps*, spinous process ; *EL*, longitudinal elastic band ; *SS*, skeletogenous layer ; *Ob*, upper arch ; *M*, spinal cord ; *P*, pia mater ; *Ic*, intercalary pieces ; *C*, notochord ; *Ee*, primary, and *Cs*, secondary sheath of the notochord ; *Ub*, lower arch ; *Ao*, aorta ; *Fo*, median parts of the lower arches, which here enclose the aorta ventrally ; *Z*, basal processes of the lower arches.

is essentially indicated by the neural arches. In the two groups last mentioned, however, skeletogenous cells break through the primary notochordal sheath (elastica) and so invade the thick secondary sheath, which in consequence encloses cartilage cells amongst its fibres. In Chimæra calcified rings are also developed in the central part of the sheath : these are more numerous than the arches. The latter are developed as paired dorsal and ventral cartilages : they remain cartilaginous in the Cartilaginous Ganoids (Figs. 23 and 24) and Holocephali, but become densely ossified in the Dipnoi (Fig. 25). In the caudal region the hæmal arches enclose the caudal aorta and vein ; further forwards the cartilages do not meet in the middle line below, and consequently the lower arches end

on either side in a laterally-directed cartilaginous projection, or *basal process.*

The relations of the arches in **Elasmobranchs, Bony Ganoids** and **Teleosts** is similar to that above described. For the further strengthening of the vertebral column so-called *intercalary pieces* (Figs. 23, 24, 26, 28) appear between the upper and·lower arches in Cartilaginous Ganoids and Elasmobranchs, and these in the
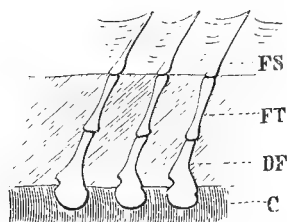


FIG. 25.—PORTION OF THE VERTEBRAL COLUMN OF *Protopterus.*
*C*, notochord ; *DF*, neural spine ; *FT*, interspinous bone ; *FS*, fin-ray.

case of the dorsal arches are often spoken of as *interneural plates.* In Elasmobranchs the neural arch may be made up of several more or less distinct pieces—the *neural processes* arising from the centrum, the *neural* and *interneural plates,* and the *neural spines.*

In the Elasmobranchii, the skeletogenous cells invade the notochordal sheath, as in the Holocephali and Dipnoi ; but the sheath then becomes segmented to form a series of cartilaginous
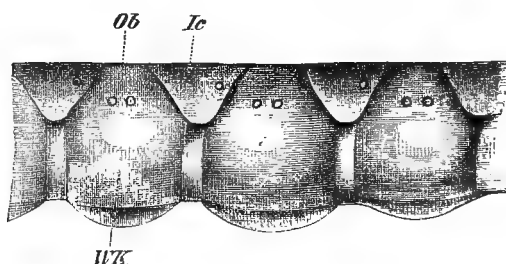


FIG. 26.—PORTION OF THE VERTEBRAL COLUMN OF *Scymnus.*

*WK*, centra ; *Ob*, upper arches ; *Ic*, intercalary pieces. The apertures for the spinal nerves are seen in the arches and intercalary pieces.

*vertebral bodies* or *centra,* which from the mode of their formation may be called *chorda-centra.* The fact is thus accounted for that the number of arch-elements does not necessarily correspond with that of the centra in these Fishes. Ossification may occur in the concave ends of the centra and in longitudinal bars along each centrum.

In Bony Ganoids and Teleosts paired dorsal and ventral cartilages likewise arise above and below the notochordal sheath, but in the course of development so extend at the base as to completely surround it. From the dorsal cartilages the upper arches take their origin, and from the ventral the lower; while the cartilage surrounding the notochord gives rise to the vertebral centra, which may therefore be distinguished from those described above as *arch-centra*.

In the development of the centra of both kinds, the notochord becomes constricted by the growth of the cartilage at regular intervals, while the latter undergoes segmentation into centra. Each point of



FIG. 27.—PORTION OF THE VERTEBRAL COLUMN OF *Polypterus*.

*WK*, centra; *BF*, basal processes; *Ob*, upper arches; *Ps*, neural spine.

constriction corresponds to the middle of a centrum, *i.e.*, it is *intravertebral* in position, and the notochord may here disappear entirely;
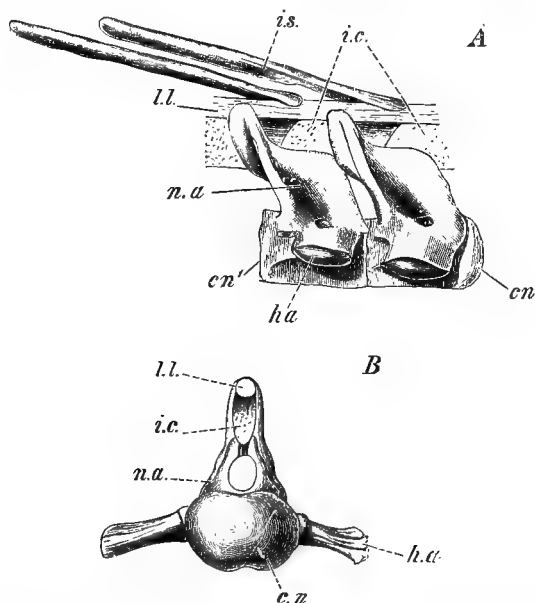


FIG. 28.—PORTION OF THE VERTEBRAL COLUMN OF *Lepidosteus*. (After Balfour and Parker.)

vertebra from anterior surface; *B*, two vertebræ from the side. *cn*, anterior convex face, and *cn*[1], posterior concave face of centrum; *h.a*, basal process; *n.a*, upper arch; *i.c*, intercalary cartilages; *l.l*, longitudinal ligament; *i.s*, interspinous bone.

*intervertebrally* it remains expanded and so persists as a kind of connecting- or packing-substance between contiguous centra, which are consequently of a deeply *biconcave* or *amphicœlous* form (Figs. 29A and 29B).

One of the Bony Ganoids, Lepidosteus, forms a marked exception to other Fishes as regards its vertebral column, inasmuch as definite *articulations* are formed between the centra. A concavity is formed at the hinder end of each centrum (Fig. 28), which articulates with a convexity on the next vertebra behind (*opisthocœlous* form). The notochord (except in the caudal region) entirely disappears in the adult; in the larva it is seen to be expanded *intravertebrally*, and constricted *intervertebrally*, a condition of things which appears again in the higher types—as, for instance,
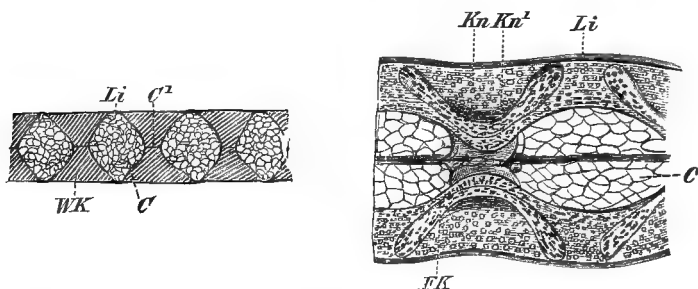


Fig. 29A.—Diagram showing the Intervertebral Remains of the Notochord.

C, C¹, expanded and constricted portions of notochord ; WK, centra ; Li, intervertebral ligaments.

Fig. 29B.—Portion of the Vertebral Column of a Young Dogfish (*Scyllium canicula*). After Cartier.

notochord ; Kn, outer, and Kn¹, inner, zone of cartilage ; FK, the fibro-cartilaginous mass lying between these zones, which is undergoing calcification ; Li, invertebral ligament.

in Reptiles. In a still earlier larval stage, however, the constrictions are intravertebral, as in other Fishes.

The vertebral column of Fishes is characterised by a very uniform character of its elements, so that a distinction can only be seen between the *trunk* and *caudal* vertebræ. Its primitive character is shown by the fact that the neural arches are usually incomplete dorsally. As a rule, the closing in of the arch is effected by special pieces of cartilage (comp. p. 38) and by an elastic longitudinal band (Figs. 24, 28) which is always present : this also applies to the hæmal arches. *Articular processes* between the arches (*zygapophyses*) are usually present in Fishes which possess bony vertebræ; in Rays and Chimæroids only amongst Fishes are definite articulations formed between the skull and

vertebral column, and in these Fishes the anterior vertebræ are fused into a single mass.

In the caudal region of Amia the centra are mostly double, an archless *pleuro-* or *post-centrum* alternating with an *inter-* or *pre-centrum*. A somewhat similar condition is found in the Jurassic Eurycormus and other fossil Ganoids.

As a rule Elasmobranchs and Ganoids possess a greater number of vertebræ (in Alopecias vulpes there are 365) than Teleosts, in which we seldom meet with more than 70 : the Eel, however, possesses more than 200.

The caudal region of the vertebral column deserves particular attention in Fishes, and the condition of this region in Amphioxus, Cyclostomi and Dipnoi, may be taken as a starting-point. In these, the notochord extends straight backwards to the hinder end of the body and is surrounded quite symmetrically by the tail-fin, which is therefore spoken of as *protocercal* or *diphycercal* (Fig. 30). This condition is also met with in many Fishes of the
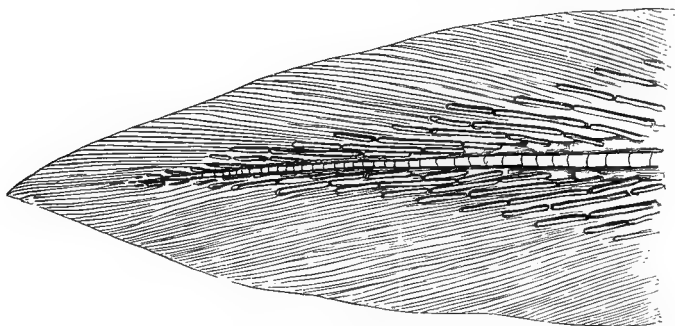


FIG. 30.—TAIL OF *Protopterus.*

Devonian strata as well as in young stages of Teleostei. In the latter, however, the ventral half of the tail-fin with its supporting skeleton (hæmal arches and fin-rays) is, as a result of unequal growth, more strongly developed than the dorsal, and the end of the vertebral column becomes bent upwards, thus giving rise to a *heterocercal* tail. This form of tail may be recognised externally, as in many Elasmobranchs, Ganoids, and numerous fossil Fishes ; or may be masked by a more or less symmetrical tail-fin, as in Lepidosteus (Fig. 31), Amia, and more particularly in most Teleosts[1] (*e.g.* Salmo, Fig. 32), in which the heterocercal character is only visible internally. The posterior end of the vertebral column is then frequently represented by a rod-like *urostyle*, and in Teleosts one or more wedge-shaped *hypural bones* (enlarged hæmal arches) generally occur directly beneath it (Fig. 32).

[1] The term *homocercal* is sometimes used to describe the masked heterocerca condition of the tail in-Teleostei.

**Amphibia.**—The vertebral column of Urodeles may be differ-
entiated into *cervical, thoraco-lumbar, sacral,* and *caudal* regions,
and these regions can be recognised, except in certain modified
forms, in all the higher Vertebrates.    On account of the absence
of extremities in Cæcilians, the vertebral column can only be
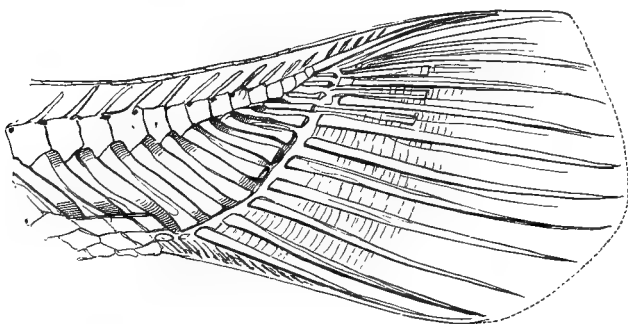


FIG. 31.—TAIL OF *Lepidosteus.*

divided into three regions—cervical, thoracic, and a very short
caudal.    In Anura, no special lumbar region can be recognised,
and the caudal portion is modified to form a urostyle (see pp. 41 and
44).   The centra of the Amphibia, as well as those of the
Amniota, correspond to *arch-centra* (see p. 39).
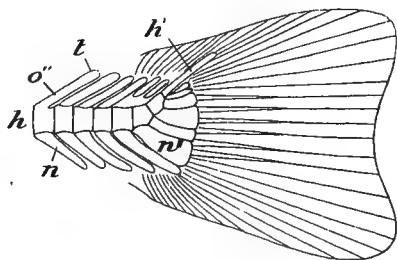


FIG. 32.—CAUDAL END OF VERTEBRAL COLUMN OF SALMON.    (From Boas's
*Zoology.*)

*h*, centrum ; *h'*, urostyle ; *n*, hæmal arch ; *n'* hypural bone ; *o''*, neural arch ; *t*,
neural spine.

The notochord of Urodele larvæ, like that of most Fishes,
undergoes intravertebral constrictions, while intervertebrally it
grows thicker, and accordingly appears expanded.    Thus the
vertebræ here also are *amphicœlous.*    Later, intervertebral masses
of cartilage become developed, which, together with the bone
which is formed at the same time in the surrounding connective-

tissue, extend inwards towards the centre, gradually constricting
the notochord so that it may eventually become entirely
obliterated. Finally a differentiation, as well as a resorption,
extending inwards from the periphery, occurs in these cartilaginous
parts : in the interior of each an *articular cavity* is formed, so that
in the vertebræ of the higher Urodeles an anterior convexity and
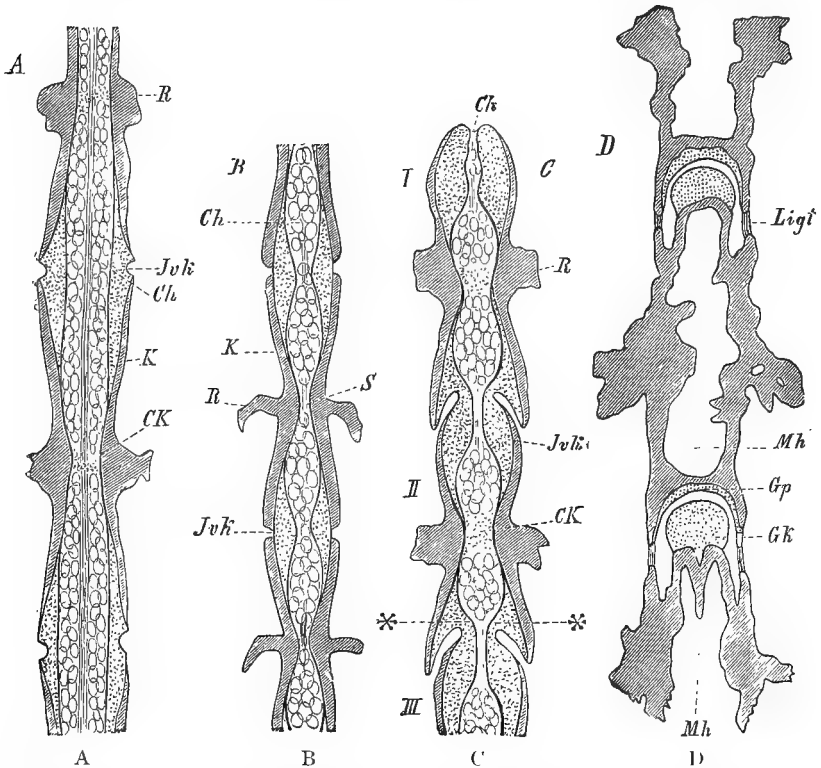


FIG. 33.—LONGITUDINAL SECTION THROUGH THE VERTEBRAL COLUMN OF VARIOUS
URODELES. A, *Ranodon sibericus* ; B, *Amblystoma tigrinum* ; C, *Gyrinophilus
porphyriticus* (the three anterior vertebræ, *I, II, III*) ; D, *Salamandrina
perspicillata*.

*Ch*, notochord ; *Jvk*, invertebral cartilage : *CK*, vertebral cartilage and fat-cells ;
*K*, peripheral bony covering of centrum ; *R*, ribs and transverse processes ; *S*,
vertebral constriction of notochord in *Amblystoma tigrinum*, without cartilage
and fat-cells in this region ; **, intervertebral cartilaginous tracts ; *Mh, Mh*,
narrow cavities ; *Gp, Gk*, articular socket and head : *Ligt*, intervertebral
ligaments.

a posterior concavity may be distinguished, both covered with
cartilage ; they are, therefore, *opisthocœlous.* A glance at Fig. 33,
A to D, will make this clear.

In the development of the vertebral column of Urodeles we
can thus distinguish three stages :—(1) A connection of the indi-

vidual vertebræ by means of the intervertebrally expanded notochord; (2) a connection by means of intervertebral masses of cartilage; and finally (3) an articular connection. These three different stages of development find a complete parallel in the phylogeny of tailed Amphibians, inasmuch as many of the Stegocephala of the Carboniferous period, as well as the Perennibranchiata, Derotremata, and many Salamanders, possess simple biconcave vertebræ without differentiation of definite articulations.[1] .

The bony parts of the vertebræ of Urodeles are not formed from the cartilaginous sheath of the notochord, but in the surrounding connective-tissue, there being only an intervertebral cartilaginous zone, extending into the ends of the centra. In the Anura, on the other hand, as in Elasmobranchs, Teleosts, bony Ganoids, and the higher Vertebrata, the vertebræ are preformed in cartilage, and true articulations always arise between the vertebræ: as a rule the convexity is posterior and the concavity anterior (*procœlous* form). A further difference is seen in the relations of the notochord, which persists *intravertebrally* longer than intervertebrally, a condition which leads towards the Reptiles.

The configuration of the caudal region of the vertebral column must also be remarked upon, as it differs in tailed and tailless Amphibians. The long caudal portion of the vertebral column in Frog larvæ, which is very similar to that of Urodeles, undergoes during metamorphosis a gradual retrogressive change, and the vertebræ of its proximal end become fused together and ossified to form a long unsegmented dagger-like bone, the *urostyle* (Fig. 34).



FIG. 34. — VERTEBRAL COLUMN OF *Discoglossus pictus.*

*Pa,* articular processes; *Ps,* neural spine; *Pt,* transverse processes of trunk vertebræ; *Ptc,* transverse processes of caudal vertebræ (urostyle, *Oc*); *SW,* sacral vertebra; *Ob,* upper arch of first vertebra; *Sg,* its condylar facets; *Po,* its anterior process; *R,* ribs.

Both neural and hæmal arches arise in direct continuity with the centra. Hæmal arches are, however, present in the caudal region of Urodeles only.

The neural spines, as well as the transverse processes, which are as a rule bifurcated at the base and are present from the second

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[1] In certain of the Stegocephala incomplete hoops of bone, the *inter-* and *pleuro-centra,* twice as numerous as the arches, surrounded the persistent notochord.

vertebra onwards, show the greatest variety as regards shape and size, differing in the several regions of the body. The transverse processes of the single *sacral vertebra*, which give attachment to the pelvis, are particularly strongly developed, especially in the Anura (Fig. 34).

Articular processes (*zygapophyses*, comp. p. 40) are well developed in all Vertebrates from Urodeles onwards, and consist of two pairs of projections arising from the anterior and posterior edges respectively of the neural arch. Their surfaces are covered with cartilage, and overlap one another from vertebra to vertebra like tiles on a roof : not unfrequently, in Urodeles, the neural spines also articulate with one another, and thus a well-articulated and mobile chain-like vertebral column results.

The first vertebra (and this is the only cervical vertebra of Amphibia), becomes differentiated from the others, and consists of a simple ring which articulates with the two condyles of the skull, and also with the base of the latter by means of a more or less marked process often spoken of as the "odontoid" process (Fig. 34) ; thus a freer movement between the skull and vertebral column is rendered possible. This vertebra, however, is not homologous with the first vertebra (*i.e.*, the *atlas*) of the higher Vertebrates, as is demonstrated by a study of its development, which shows that the real atlas loses its individuality as a separate mass, and becomes united with the occipital region of the skull.[1]   The first vertebra of Amphibians is therefore more nearly comparable to one of the next following cervical vertebræ of higher forms. It possesses posterior zygapophyses only, and its condylar facets correspond to modified transverse processes.

The number of vertebræ present in Urodeles is inconstant, and varies greatly : it may reach to nearly 100 (Siren), and in Cæcilians may be very much greater (up to 275). In Anura, on the other hand, there are only eight precaudal vertebræ and one sacral, in addition to the urostyle. It is evident from this fact alone that the recent forms of Urodela and Anura are widely separated from one another.

**Reptilia.**—In contrast to the numerous fossil forms, only a few existing Reptiles, viz., Hatteria (Rhynchocephala) and the Geckos (Ascalabota), retain throughout life the primitive *biconcave* character of their vertebræ, with the notochord expanded intervertebrally.

In the generalised Rhynchocephala the formation of the vertebræ out of several pieces, such as occurs amongst the Stegocephala (p. 44), is still indicated by sutures, each vertebra consisting of two processes, a centrum proper (pleurocentrum) and an intercentrum.

In all the others, the notochord remains expanded longer in the *intravertebral* regions than intervertebrally, but in the adult it be-

[1] A similar fusion of the anterior part of the vertebral column with the skull occurs in some Fishes and in Dipnoi.

comes entirely aborted and replaced by bony tissue.  This stronger
and more solid ossification of the whole skeleton forms a character-
istic difference between the Ichthyopsida on the one hand and
the Amniota on the other.  As a rule the vertebræ of Reptiles
become definitely articulated with one another, and are of the
*procœlous* type : the above-named forms, with intervertebral re-
mains of the notochord, form an exception to this rule.  In Croco-
diles fibro-cartilaginous *intervertebral discs* or *menisci* occur between
the centra (Fig. 35).

In Crocodiles the vertebræ are mostly procœlous, an exception being seen
in the two sacrals and first caudal.  In Chelonians there is great variation in
the form of the individual centra of the cervical vertebræ—even in the same
individual procœlous, opisthocœlous, biconcave, and even biconvex centra,
with intervertebral discs, may occur ; while the thoracic and lumbar vertebræ
have flattened faces, and are firmly united together by cartilage.

In the Jurassic Ichthyosaurus and Eosaurus the centra were short and
deeply biconcave, like those of Fishes, and the arches were connected with
them by cartilage and connective tissue ; as a sacrum was absent, only a
precaudal and a caudal region can be recognised.  In Plesiosaurus, Plio-
saurus, Nothosaurus, Simosaurus, the Anomodontia and others, the centra
were also biconcave or flattened.

What has been said as to the classification of the vertebræ into
different regions in Urodeles, as well as to the presence of the
various processes, usually applies here also to a still greater extent.
Except in limbless form, there are always *several* cervical vertebræ
instead of a single one : there are also typically at least *two* sacral
vertebræ.  The two first cervical vertebræ become differentiated
to form an *atlas*—usually consisting of three pieces, and an *axis*
—with an odontoid bone (Fig. 35, and comp. p.  45).[1]

The neural spines vary in size, and transverse processes arise
from the centra themselves or close to them.  Lower arches,
attached intercentrally (chevron bones) are present in the tail in
Lizards, Crocodiles, and some Chelonians; and besides these,
median inferior processes of the centra themselves (? intercentra) are
seen in many of the vertebræ of Lizards, Crocodiles, and Snakes,
and in the latter paired processes partly enclose the caudal vessels.
The arches in Snakes, Lizards, and Chelonians become united
with the centra by synostosis, while in Crocodiles they remain
separated from them by sutures (Fig. 35).

In consequence of the absence of a pectoral arch, the vertebral
column of Snakes and Amphisbænians, like that of Cæcilians,
consists of trunk and caudal vertebræ only.  The vertebral column
of Chelonians deserves particular notice as a large portion of it
becomes anchylosed with the dermal bones of the carapace (p. 33,
Fig. 21), and is thus rendered immovable.

[1] The odontoid bone corresponds morphologically to a part of a centrum of the
atlas.  A so-called *pro-atlas*—the remains of a vertebra situated between the
skull and atlas proper—is present in the Crocodilia (Fig. 35), Hatteria, and
Chamælaeo, as well as in many fossil forms.

In Snakes and some Lizards (Hatteria, Iguana) extra articular processess (*zygosphenes* and *zygantra*) are developed on the neural arches. In Hatteria and the Geckos, small separate ossifications (*intercentra*, comp. p. 43, 44, 46) are present on the ventral side of the vertebral column between many of the centra. In the caudal region of Lizards an unossified septum remains in the middle of each centrum, so that the tail easily breaks off at these points : when this happens the tail grows again, but proper vertebræ are not formed.

In fossil Reptiles, which both as regards size and number of species usually surpassed the existing representatives of the class, the sacrum often consisted of as many as four or five vertebræ. The following facts will give some idea of the monstrous proportions of these old genera of Reptiles :— *Atlantosaurus immanis*, a North American Dinosaur, reached a length of
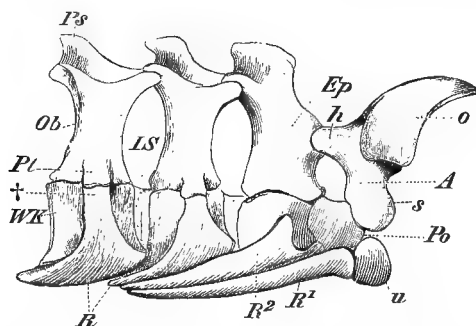


FIG. 35.—ANTERIOR PORTION OF THE VERTEBRAL COLUMN OF A YOUNG CROCODILE.

*WK*, centrum ; *Ob*, neural arch ; *Ps*, neural spine ; *Is*, intervertebral disc ; *Pt*, transverse process, arising from the base of the arch and articulating with the rib (*R*, *R¹*, *R²*) at † ; *A*, atlas ; *a*, ventral element, and *s* arch of atlas ; *o*, " pro-atlas " ; *Ep*, axis, articulating with the atlas at *h* ; *Po*, odontoid process.

about 80 feet, and the transverse diameter of the individual vertebræ amounted to 16 inches, while *Apatosaurus laticollis*, found in the same strata, possessed cervical vertebræ which reached a diameter of 3½ feet.

A knowledge of fossil genera of Reptiles is of the greatest interest, as in many groups important points of connection with Birds can be recognised.

**Birds.**—The vertebral column of Birds corresponds with that of Reptiles not only in its phylogenetic relations, but also ontogenetically. In both groups the notochord eventually disappears entirely, and the whole skeleton becomes strongly ossified. Archæopteryx, as well as Ichthyornis (from the American Cretaceous), possessed *biconcave* vertebræ, but in existing Birds this character never occurs except in the free caudal vertebræ (p. 49). Cervical, thoracic, lumbar, sacral, and caudal regions can be distinguished. The arches always become united into a single mass with the corresponding centra, and are no longer separated from

them throughout life by sutures, as is the case in certain Reptiles:
even the ligament which keeps the odontoid process of the axis
in its place may become ossified. Fibro-cartilaginous discs or
menisci are present between the centra. In the cervical region,
which is extremely flexible and often very long, the centra are
in nearly all cases connected by means of *saddle-shaped synovial
articulations;* the upper part of the bifurcated transverse processes
arises from the arch, the lower from the centrum, and these may
unite with the corresponding forked rib, the vertebral artery and
vein extending through the foramen thus formed (Fig. 36).

In the thoracic and lumbar regions more or fewer of the
vertebræ usually become immovably united together.

The sacral region in Bird-embryos, like that in existing adult
Reptiles, consists of *two* vertebræ only, the transverse processes of
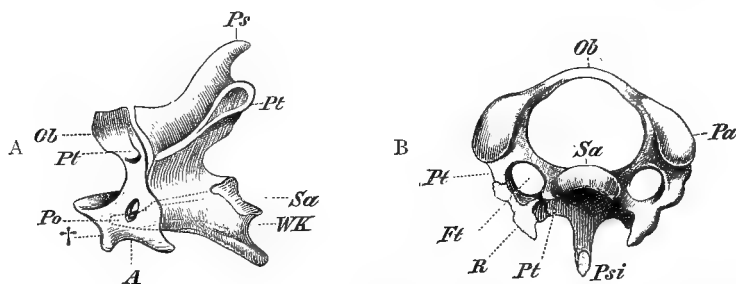


FIG. 36, A.—ATLAS AND AXIS (from the left side); and B, THIRD CERVICAL
VERTEBRA (ANTERIOR FACE) OF WOODPECKER (*Picus viridis*).

A. *Ob*, *A*, arch and centrum of atlas; †, condylar facet; *Po*, odontoid process;
   *WK*, centrum of axis, and *Sa*, its saddle-shaped articular surface for the
   third vertebra; *Ps*, neural spine of axis; *Pt*, transverse process.
B. *Sa*, articular surface of centrum; *Ob*, upper arch; *Pa*, articular process; *Pt*, *Pt*,
   the two bars of the transverse process, shown on one side anchylosed with
   the cervical rib (*R*); *Ft*, vertebrarterial foramen; *Psi*, median inferior pro-
   cess (hyparpophysis).

which ossify separately and correspond to fused ribs, as in
Amphibians and Reptiles. During further development, however,
a number of other (*secondary* sacral) vertebræ (thoracic, lumbar,
and caudal), with their rudimentary ribs, become fused with the
two *primary* ones (Fig. 37), so that the entire number of vertebræ
in the sacrum may be as many as twenty-three. In Archæopteryx
the sacrum was much shorter than in existing Birds, and fewer
vertebræ were united with it.

In existing Birds the caudal region always exhibits a more or
less rudimentary character, and in its posterior portion the ver-
tebræ usually fuse together to form a flattened bone, the *pygostyle*,
which supports the tail quills (Fig. 111). An exception to this rule
is found only amongst the Ratitæ, in which all the caudal vertebræ

remain distinct. That the latter is the more original condition in Birds is shown by a study of their development as well as by the condition of the tail in Archæopteryx, in which it was supported by numerous elongated free vertebræ (Fig. 38). Moreover, in many Birds (*e.g.* Psittacus undulatus) more vertebræ are formed in the embryo than are seen in the adult. It must, however, be borne in mind that the pygostyle may be made up of from six to ten

fused caudal vertebræ, and in the sacrum even a greater number may be included (cp. p. 48): thus in the common Duck, seven become united with the pelvis, eight remain free, and the pygostyle is composed of ten separately ossified and fused segments, making in all twenty-five vertebræ originally present in the caudal region of this Bird.

**Mammalia.**—The notochord here persists longer *intervertebrally* than intravertebrally, but it disappears entirely by the time the adult condition is reached. A jelly-like pulpy mass, the *nucleus pulposus*, persists, however, throughout life in the centre of the fibro-cartilaginous menisci which are developed between the centra. The whole vertebral column is preformed in cartilage, and the centra develop in continuity with the arches but become ossified from separate centres, as do also the various processes. These ossifications, however, become fused together in the adult. The presence of bony discs or *epiphyses* on the ends of the centra which unite with the latter comparatively late, is very characteristic of Mammals ; they are however absent or only imperfectly developed in Monotremata and in existing Sirenia.

True articulations between the centra are never formed, except on the atlas and anterior face of the axis; but as in Amphibians, Reptiles, and Birds, well-developed articular processes (zygapophyses) are present, arising from the neural arches.[1] The cervical region is usually the most moveable, and the centra may be so much hollowed out in this region as to give them an opisthocœlous character (*e.g.* Ungulata). In some cases, on the other hand, the
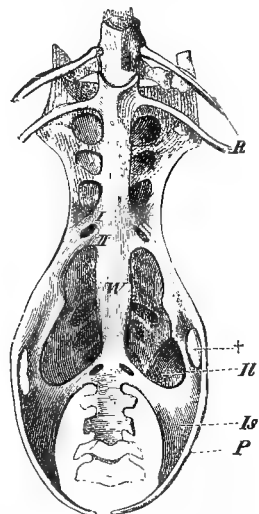


FIG. 37.—PELVIS OF OWL (*Strix bubo*). Ventral view.

*W*, position of the primary sacral vertebræ : between *R* and *Il*, and behind *W*, are seen the secondary sacral vertebræ, fused with the primary (*W*); *Il*, ilium ; *Is*, ischium ; *P*, pubis ; +, foramen between ilium and pubis ; *R*, last two pairs of ribs.

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[1] In certain Edentata (*e.g.* Myrmecophaga, Dasypus) extra articular processes are present besides the ordinary zygapophyses on the posterior thoracic and lumbar vertebræ (Fig. 39B.).

cervical vertebræ may become firmly fused together (Cetacea). The distal parts of the transverse processes, representing rudimentary ribs, are perforated by the vertebrarterial canal (p. 48): in Monotremes these remain distinct at any rate for a long time.



FIG. 38.—*Archæopteryx lithographica.*  From the Solenhofen slates (Jurassic.) After Dames, from the specimen in the Berlin Museum.

The atlas and axis essentially resemble those of Birds, but the differentiation of the vertebral column into regions characterised by difference of form is much more sharply marked than in any other Vertebrates.   There are as a rule *seven* cervical vertebræ; Bradypus, however, possesses eight to nine, and Tamandua bivittata eight, while in Manatus and Cholœpus there are only six.

The transverse processes are simple in all but the cervical region and arise from the base of the arch: in the thoracic region they are tipped with cartilage on the ventral side of their distal ends for articulation with the tubercle of the rib (p. 58). In the lumbar and sacral regions they arise from the centra, and contain fused rib-elements.

In long-necked Ungulates (*e.g.* Horse, Camel, Ox) the neural spines of the anterior thoracic vertebræ are greatly developed, and a correspondingly strong cervical ligament (ligamentum nuchæ) is particularly well developed to support the weight of the head. This is also true of antler-bearing animals and of the Gorilla.

The number of thoracolumbar vertebræ varies greatly in different Mammals: there may be as few as fourteen (Armadillo) or as many as thirty (Hyrax). In Ungulates the number is constantly nineteen. In the lumbar vertebræ the transverse processes are especially long, and other processes (anapophyses, metapophyses, hypapophyses) are characteristically present in this region.

Thus, as in Amphibians, Reptiles and Birds, the pelvis is connected with the sacrum by means of rudimentary ribs. As in the two last-mentioned groups, there are not more than *two* primary sacral vertebræ, but except in Ornithorhynchus and most Marsupials a few caudal become later included in the sacrum and are usually more or less closely united



FIG. 39A.—DIAGRAM SHOWING MODE OF OSSIFICATION OF HUMAN AXIS. (Ventral surface.) From Flower's *Osteology of the Mammalia.*

*o*, odontoid process, or centrum of atlas ; *c*, proper centrum of axis ; *na*, neural arch ; *as*, anterior articular surface ; *e, e, e, e,* epiphyses, completing the ends of the centra.
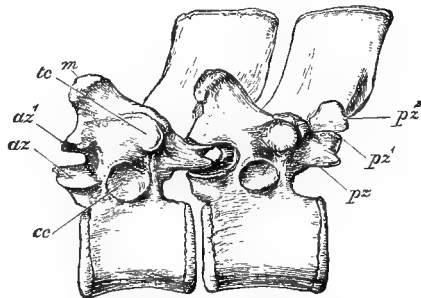


FIG. 39B. SIDE VIEW OF THE TWELFTH AND THIRTEENTH THORACIC VERTEBRÆ OF GREAT ANTEATER (*Myrmecophaga jubata*), ⅔. From Flower's *Osteology of the Mammalia.*

*m*, metapophysis ; *tc*, facet for articulation of tubercle of rib ; *cc*, ditto for capitulum of rib ; *az*, anterior zygapophysis ; *az*¹, additional anterior articular facet ; *pz*, posterior zygapophysis ; *pz*¹ and *pz*², additional posterior articular facets.

with it by synostosis. The various processes of the sacral vertebræ are more or less reduced. In Anthropoids, as in Man, the first sacral vertebra is plainly marked off from the last lumbar by the formation of the so-called *promontory.* A sacrum is wanting in

E 2

the Cetacea and Sirenia, in correspondence with the absence of hind-limbs.

The caudal vertebræ vary extremely in their development, and excepting in most long-tailed Mammals—such as Kangaroos, Sirenians, Cetaceans and certain Apes—no longer develop lower arches. When present these " chevron bones " are intervertebral in position.

The greatest number of caudal vertebræ is found in Microgale longicauda (forty-eight), Manis macrura (forty-six to forty-nine), Paradoxurus (about thirty-six), and certain Monkeys (thirty-two to thirty-three).

The caudal region is most reduced in the higher Primates, in which it gives rise to a stump-like *coccyx* consisting of at most five to six rudimentary vertebræ, all fused together, and these may even (in the human subject, especially in the male) fuse with the sacrum. Many facts as regards the development as well as the structure of the whole tail-region in the adult show however that the ancestors of Man must have been provided with a distinct and functional tail.

## II. Ribs.

The ribs do not as a general rule (with the exceptions to be noted presently) arise as outgrowths from the vertebral column, but become developed independently in the skeletogenous layer—that is, in the tissue of the somites, and their connection with the vertebral column is a secondary one. They stand in the closest connection with the intermuscular septa or myocommata of the great lateral muscles of the body (Fig. 40 A,) are arranged segmentally, and onto- as well as phylogenetically, pass through a membranous, a cartilaginous, and a bony stage : their ossification is independent of that of the vertebral column. In their primitive form, the ribs have simple, unbifurcated heads, the articulation of which with the vertebral column first takes place in the region of the " intercentra " (p. 47), and from this condition all the later modifications as regards their form and connection are to be derived.

The ribs present great variation in the various vertebrate Classes : they may be short and stump-like and almost horizontal in position, or may grow ventralwards so as to encircle the body-cavity. Primitively, ribs may be present all along the vertebral column, but in the higher types they become reduced in certain regions.

In order to arrive at sound conclusions as to the morphological value of the ribs, their relations to the soft parts must be taken into consideration. It is then seen that they *are not completely homologous throughout the vertebrate series*, and that those of Ganoidei, Teleostei and Dipnoi are not exactly comparable to those of Elasmobranchii, Amphibia, and Amniota (Fig. 40A).
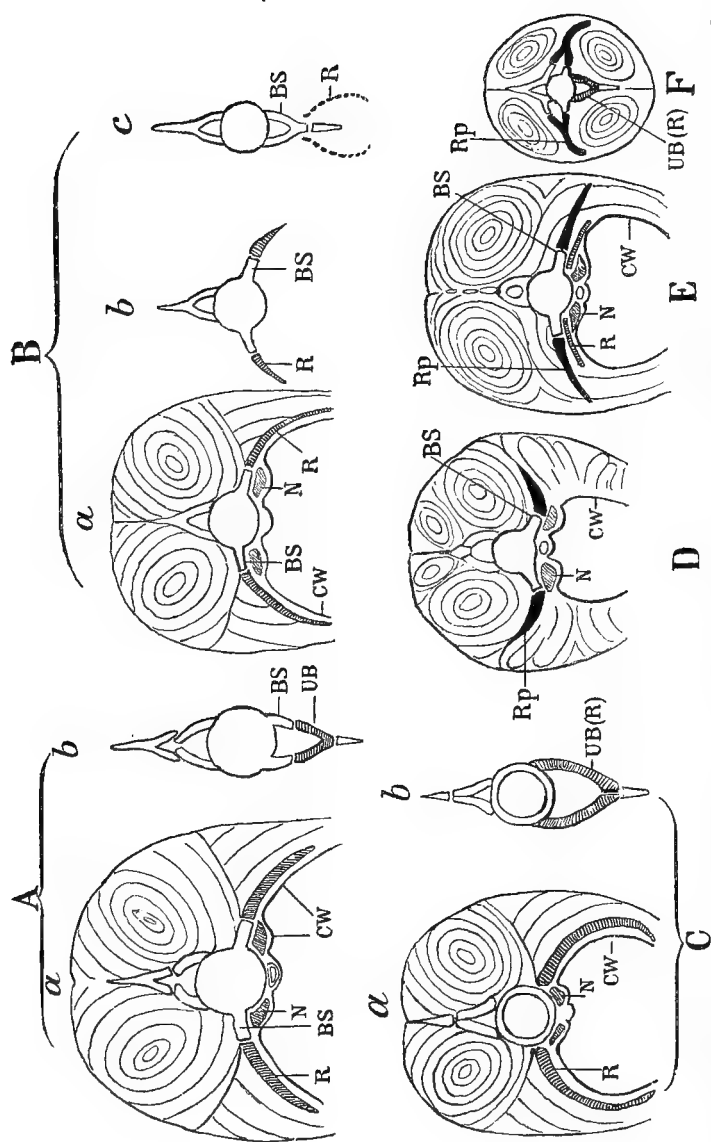
Fig. 40A.—Diagrammatic Transverse Section of various Vertebrates, showing the relations of the ribs and hæmal arches. Homologous parts are similarly shaded. A—Ganoidei, B—Teleostei, C—Dipnoi, D—Elasmobranchii, E—Polypterus, F—Amphibia (Urodela), through the base of the tail.

N, kidneys; CW, wall of cœlome; BS, basal processes; R, ribs characteristic of most Fishes ("lower ribs"), which also appear in the form of hæmal arches in the caudal region of Urodeles (F, UB(R)); UB, hæmal arches; Rp, ribs characteristic of Elasmobranchii Amphibia, and Amniota ("upper ribs"). The figures also show the dorso-lateral and the ventro-lateral muscles. In B.a, the small cartilages beneath the lateral line referred to in the text are not indicated.

**Ganoidei, Teleostei,** and **Dipnoi**—In these forms the ribs, almost without exception, are connected with the ventral parts of the notochordal sheath (Dipnoans) or with the " basal processes " (Ganoids and Teleosts, see p. 38).[1]   This is one point of difference between the ribs of these forms and those of other Vertebrates: another is that they are always situated beneath (internal to) the lateral muscles, between these and the peritoneum (Fig. 40A, A, B, C).   In Teleosts the ribs are at first continuous with the basal processes and become secondarily segmented off from them : this may be a cœnogenetic modification.

Towards the caudal region, the ribs gradually take on the form of hæmal arches, which have precisely the relations of the ribs as
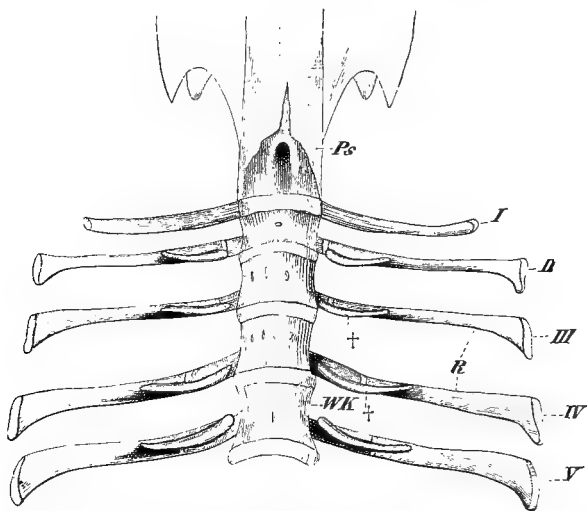


Fig. 40b.—Anterior End of the Vertebral Column of Polypterus.   From the ventral side.

*WK*, centra ;   *I—V*, first five pairs of dorsal ribs ;   ††, ventral ribs.

described above.   In Teleosts, however, the ribs gradually disappear in passing backwards to the tail, and the hæmal arches are formed by the basal processes alone (Fig. 40A, B, *c.*).   In spite of these differences, however, there can be no doubt that the ribs of Teleosts are homologous with those of Dipnoans and Ganoids.

Large rib-like structures (" upper ribs ") are present in Polypterus (Fig. 40b), which have a similar position to that of the ribs in the forms next to be described ; and amongst the Teleostei (Clupeoidei, Salmonidæ) small cartilages are present beneath the lateral line in a similar position to that of the distal

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[1] The ribs are rudimentary in certain species of all the orders of Fishes, and in some cases their place is taken by fibrous bands, arising from the skeletogenous layer.   They are wanting in Cyclostomes.

ends of the upper ribs of Polypterus, to which they probably correspond. There can be little doubt, however, that the more delicate bars which lie ventrally to the larger structures in Polypterus correspond to the ribs of Fishes ("lower ribs") as described above. It is therefore possible that Polypterus and certain Teleostei possess the representatives of two sets of ribs—the one corresponding to those of the majority of Fishes, and the other to those of Elasmobranchs, Amphibians, and Amniota (Fig. 40A, E).

The *intermuscular bones* present in the myocommata of Teleosts probably correspond simply to ossifications of the septa, and have nothing to do with ribs.

**Elasmobranchii.**—The small, cartilaginous ribs of these Fishes arise independently of the vertebral column in the connective tissue of the intermuscular septa, and extend outwards between the dorso-lateral and the ventro-lateral muscles (see Fig. 40 A, D). They are thus not genetically connected with the basal processes, although they early become united to them by ligament, and therefore do not correspond either to differentiations of the hæmal arches or to transverse processes segmented off from these.

**Amphibia.**—The ribs of Amphibians arise in a very similar manner to those of Elasmobranchs, but differ from them in being from the first connected with the neural (dorsal) and not with the hæmal (ventral) arches or basal processes. This is due to the phylogenetic upward displacement of the longitudinal septum separating the dorso-lateral from the ventro-lateral muscles. Like those of Elasmobranchii and Amniota, the ribs are situated between these two masses of muscle, but never extend very far laterally or ventrally.

The ribs of Urodeles are forked at their proximal ends, and articulate with bifurcated transverse processes of the vertebræ arising from the arch and centrum respectively : the dorsal part of the transverse process, arising from the arch, is a new acquisition. In many cases ribs are present only in the region of the trunk, but occasionally they extend into the base of the tail, where hæmal arches, corresponding to the basal processes of Elasmobranchs, are also present[1] Urodeles therefore possess the representatives of two kinds of ribs, morphologically distinct from one another (comp. Polypterus and Teleostei, p. 54). All the precaudal vertebræ except the first usually bear ribs ; in rare cases (Spelerpes) there are a few ribless lumbar vertebræ.

In the Anura the ribs are much shorter, and are doubtless degenerated. As a rule, they become fused with the broad transverse processes, at the ends of which they are situated ; the anterior ones may sometimes, however, remain distinct (Fig. 34). They are never bifurcated, and no trace of hæmal arches exists.

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[1] The elements of true ventral arches (basal processes) may also be present all along the trunk in the larva of Salamandra maculosa, and are still more marked in Necturus (Menobranchus).

In the Urodele Necturus four cartilaginous "*abdominal ribs*" (see below) may be present in the septa between the ventral parts of the myotomes on the level of the shoulder-girdle. Bony abdominal ribs also occur in certain Stegocephala.

**Reptiles**. As already mentioned, the ribs of the Amniota are comparable to those of the Amphibia, but they grow further ventralwards and so encircle the body-cavity to a greater or less extent. The dorsal (proximal) section of the rib may also become segmented from the distal (ventral) portion ; and as a rule a certain number of the ribs unite together ventrally to form a *sternum* (Fig. 44) : these are usually distinguished as " true " ribs from the others, or " false " ribs.

The ribs of Snakes show the least amount of differentiation ; for, without giving rise to a sternum, they extend along the whole trunk from the third cervical vertebra to the anus, and retain throughout a similar form and size. In Lizards, where a dorsal, unforked, bony and a ventral cartilaginous portion can be distinguished, three or four ribs reach the sternum, and are not always completely segmented off from it.

In Chelonians the cervical ribs unite with the vertebræ more or less completely, and in the region of the trunk the ribs become fused with the costal plates of the carapace (p. 33). Their proximal unbifurcated ends are attached between the centra, at the junction of centrum and arch. There is no sternum.

The proximal ends of the cervical ribs in the Crocodilia are bifurcated, in correspondence with the double transverse processes in this region, and thus a vertebrarterial canal is formed. Further back, the ribs increase in length, and become segmented into two or three articulated portions. In passing from before backwards, their point of origin becomes gradually shifted, so that while the anterior thoracic ribs are attached to the centra, the posterior ones arise entirely from the transverse processes, which increase in size correspondingly. Eight or nine ribs reach the sternum, and from the eighteenth vertebra backwards the transverse processes no longer bear ribs, but only short cartilaginous apophyses.

*Uncinate processes* (see below) are present in connection with the ribs in the Crocodilia as well as in Hatteria.

" *Abdominal ribs*," arising as ossifications of the inscriptiones tendineæ of the ventral muscles, occur in Crocodiles and in Hatteria, as well as in numerous fossil Reptiles.

**Birds**.—The ribs of Birds exhibit a much more marked segmentation into *vertebral* and *sternal portions*, both of which become ossified, and this evidently stands in relation to their more active respiration. *Uncinate processes*, moreover, arise from the vertebral portions in nearly all Birds, and overlap the ribs next behind them (Fig. 41). The whole costal apparatus

is rendered still firmer by the frequent fusion of the vertebræ (p. 48), by the individual ribs often being very broad, as well as by the form and arrangement of the sternum and pectoral arch, which will be treated of later. The last three or four cervical vertebræ may bear comparatively large and movable ribs. The
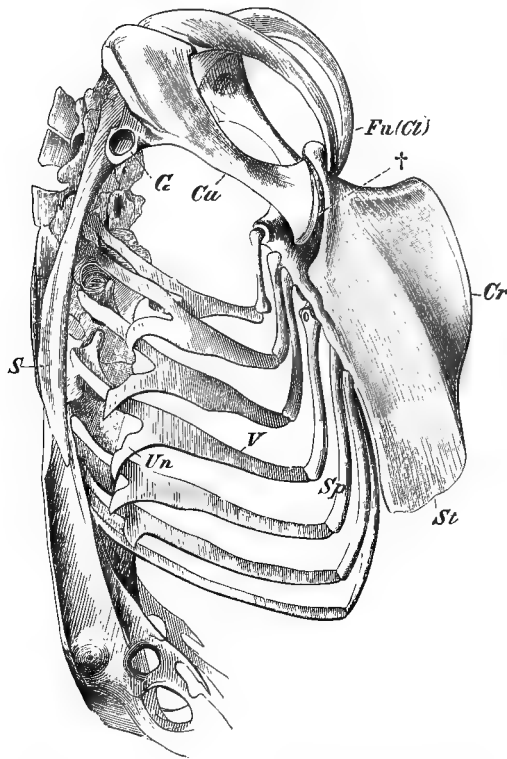


FIG. 41.—SKELETON OF THE TRUNK OF A FALCON.

*S*, scapula ; *G*, glenoid cavity for humerus ; *Ca*, coracoid, which articulates with the sternum (*St*) at † ; *Fu(Cl)*, furcula (clavicles) ; *Cr*, keel of sternum ; *V*, vertebral, and *Sp*, sternal, portion of rib ; *Un*, uncinate process.

number of ribs which articulate with the sternum varies between two (Dinornis elephantopus) and nine (Cygnus).

(Concerning the sacral ribs, see p. 48.)

Archæopteryx possessed 12–13 pairs of "abdominal ribs" (comp. p. 56).

**Mammals.**—The cervical ribs here unite completely with the vertebræ, and a vertebrarterial canal is thus formed, as in Crocodiles and Birds. There is considerable variation with regard to the

number of ribs which reach the sternum, and in some cases the sternal, as well as the vertebral ribs may become ossified.   In both "true" and "false" ribs (p. 56), a *capitulum*, a *neck*, a *tuberculum*, and a *body* may be distinguished (Fig. 42). The capitulum of the former usually articulates with its own centrum as well as with that next in front, in the region of the epiphysis ; the tuberculum articulates with the cartilaginous facets on the transverse process. In the "false" ribs, these characters are to a greater or less extent lost. As already mentioned (p. 51), rudiments of ribs are present in the lumbar and sacral regions, and unite with the corresponding transverse processes.



FIG. 42.—COSTAL ARCH OF MAN.

*WK*, centrum of vertebra ; *Pt*, transverse process ; *Ps*, neural spine ; *Cp*, body of rib ; *Ca*, capitulum ; *Co*, neck ; *Tb*, tuberculum ; *Kn*, cartilaginous sternal rib ; *St*, sternum.

This fact, as well as the rudimentary character and variety in size of the eleventh and twelfth ribs and the occasional presence of a thirteenth rib in Man, shows that a reduction in the number of these structures is here taking place : a gradual shortening of the thoracic portion of the vertebral column and a corresponding lengthening of the cervical and lumbar regions. is also taking place in Mammals generally, and thus it may be stated that the reduction in the number of ribs is correlated with a higher stage in development of the Vertebrate body.

### III. STERNUM.

Never present in Fishes, the sternum appears for the first time in **Amphibians** in the form of a small variously-shaped plate of cartilage situated in the middle line of the chest (Fig. 43). It arises as a paired cartilaginous plate [1] in the inscriptiones tendineæ of the rectus abdominis muscle, and therefore may be looked upon as corresponding to a pair of "abdominal ribs." Such cartilaginous abdominal ribs must have been present in greater numbers in the ancestors of existing Urodeles (comp. Necturus, p. 56). In many tailless Batrachians (*e.g.*, Rana) the ventral portion of the pectoral arch is continued forwards in the middle line, from where the two clavicles meet, as a slender *omosternum* (Fig. 43, D) : this has a similar origin, and the proximal portion both of it and of the sternum become ossified. Thus the sternum and omosternum of Amphibians are not to be considered as correspond-

[1] It is unpaired from the first in Triton and Rana, but this is probably due to an abbreviation of development.
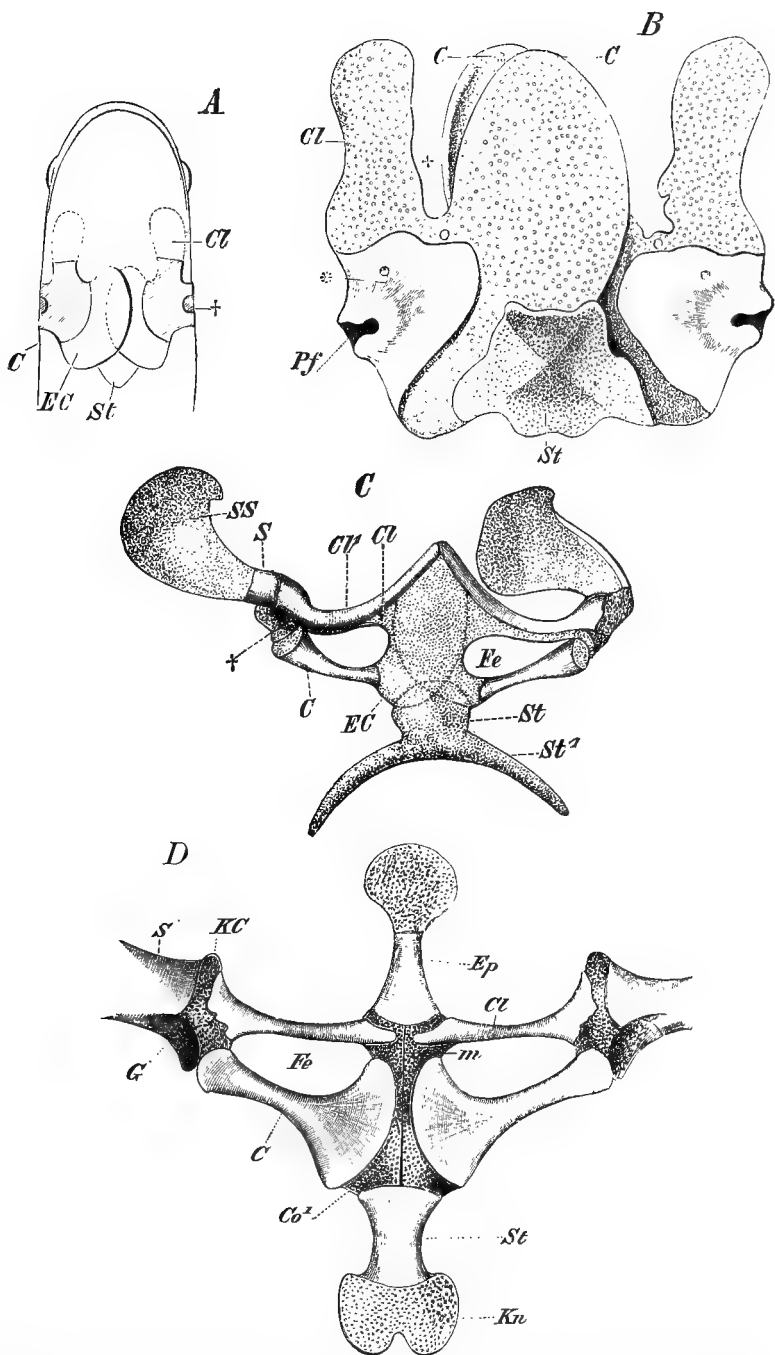
FIG. 43.—PECTORAL ARCH OF VARIOUS AMPHIBIANS. (From the ventral side). A—Urodele (diagrammatic); B—Axolotl; C—Bombinator igneus; D—Rana esculenta.

SS, suprascapula; S, scapula; Cl, procoracoid; Cl¹ (Cl in D), clavicle; C, coracoid; EC, Co¹, epicoracoid; †, Pf, G, glenoid cavity for the humerus; St, Sn, sternum; Ep. omosternum; Fe, fenestra between procoracoid and coracoid bars. * and † in B indicate nerve-apertures.

ing to differentiations of the pectoral arch,[1] but as consisting of skeletal parts which primarily belong to the body-wall, and only secondarily come into connection with the limb-skeleton.

In most Urodeles and certain Anurans the edges of the cartilaginous sternum are inserted into the grooved median margins of the two coracoids (Fig. 43, B, C), to which they are united by connective tissue.  In Rana, on the other hand (D), in which the two halves of the pectoral arch are much more closely connected in the middle line, by far the greater part of the sternum lies entirely posterior to the coracoids.  In the Perennibranchiata and Derotremata the sternum is much simpler than in other Amphibians, and in Proteus and Amphiuma it undergoes complete degeneration.
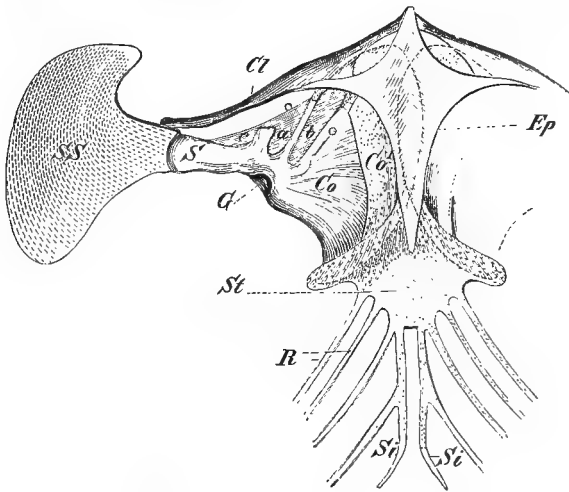


FIG. 44.—PECTORAL ARCH AND STERNUM OF A GECKO
(*Hemidactylus verrucosus*).

*St*, sternum ; *R*, ribs ; *Si*, cartilaginous cornua to which the last pair of ribs is attached ; *SS*, suprascapula ; *S*, scapula ; *Co*, coracoid ; *Co*[1], cartilaginous epicoracoid : *Ep*, episternum ; *a*, *b*, *c*, membranous fenestræ in the coracoid ; *Cl*, clavicle ; *G*, glenoid cavity for the humerus.

Nothing is known with regard to the sternum of fossil Amphibians, which was probably entirely cartilaginous.

In the **Amniota,** the sternum arises by a number of ribs on either side of the middle line running together to form a continuous cartilaginous tract.  An unpaired cartilaginous sternal plate is formed by the tract of either side becoming more or less completely fused with its fellow, and from this plate the ribs become secondarily segmented off by the formation of true articulations.

[1] It has been recently shown that in the Elasmobranch *Notidanus* cartilages are present in the median ventral line of the pectoral arch which are segmented off from the coracoids.

Later it may become calcified (Reptiles), or converted into true bone (Birds, Mammals). In Reptiles, Birds, and Monotremes the coracoids, as in Amphibians, always come into direct connection with the lateral edges of the sternum (comp. Figs. 41, 44, and 48).

The sternum is greatly developed in Birds, and consists of a broad more or less fenestrated plate, provided in the vast majority of Carinatæ with a projecting keel, which forms an additional surface for the origin of the wing-muscles (Fig. 41). In contrast to these, the cursorial Ratitæ are characterised by a broad, more or less arched, shield-like sternum without a keel. In some flightless Carinatæ, however, the keel is rudimentary or even absent, and a keel may occasionally appear, though not constantly,
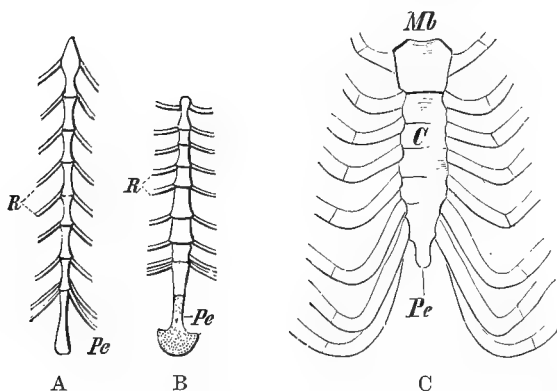


FIG. 45.—A, STERNUM OF FOX ; B, OF WALRUS ; AND C, OF MAN.

*Mb*, manubrium ; *C*, body ; *Pe*, xiphoid process ; *R*, ribs.

in certain Ratitæ. The presence or absence of a keel is not, therefore, a constant character separating these two groups of Birds from one another.[1]

A greater number of ribs are as a rule concerned in the formation of the sternum of Mammals than is the case in Reptiles and Birds. Consisting at first of a simple cartilaginous plate, the sternum later becomes segmented into definite bony portions (sternebræ) the number of which may correspond to the affixed ribs (Fig. 45, A, B). But in other cases, as, for instance, amongst Primates (C), the individual bony segments may run together to form a long plate (*corpus sterni*). The anterior end of the sternum becomes differentiated into the so-called *manubrium*, and the posterior end into the *xiphoid* or *ensiform process*. The latter owes its origin in the embryo to the ventral fusion of a true pair of ribs.

[1] A keel was also present in the flying Reptile *Plesiosaurus*, and may be developed wherever a larger surface for the origin of the pectoral muscles is required (*e.g.*, Cheiroptera).

### IV. EPISTERNUM.

Episternal structures, which are wanting in Fishes, Dipnoans and recent Urodeles, play an important part in fossil Amphibians
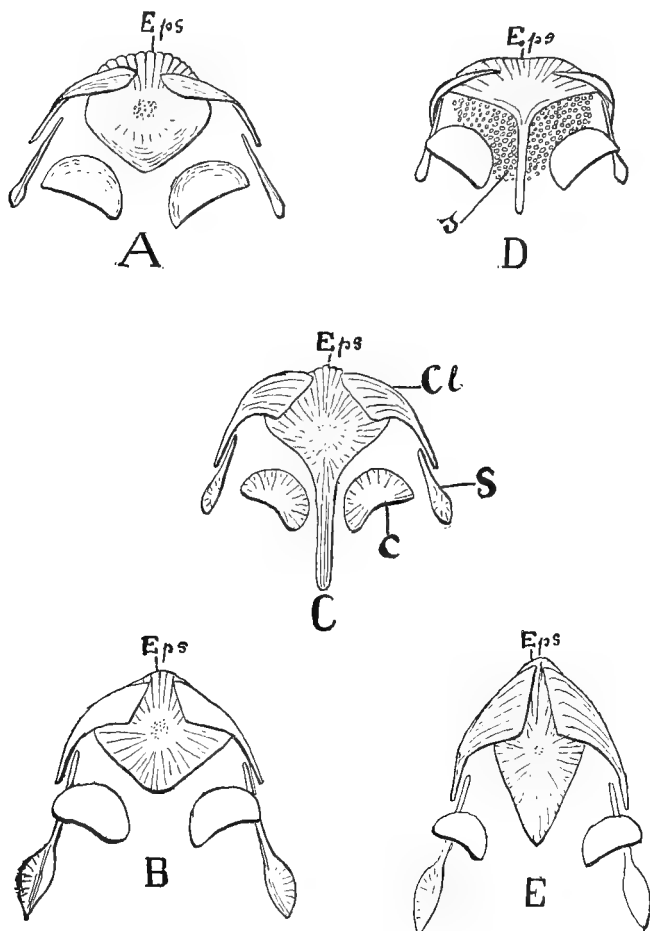


FIG. 46.—PECTORAL ARCH OF VARIOUS STEGOCEPHALA (from the ventral side). After H. Credner.

A, Branchiosaurus, × 3 ; B, Pelosaurus × 2 ; C, Discosaurus, × 2 ; D, Hylonomus, × 2 ; E, Archegosaurus, × about ¼.   *Eps*, episternum ; *Cl*, clavicle ; *s*, scapula ; *c*, coracoid ; *s*, calcification in the sternum or in the cartilage of the coracoid.

and primitive Reptiles (*e.g.*, Stegocephala and Palæohatteria), in which, both as regards form and structure, they bear a great resemblance to the episternum of certain existing Reptiles.

In the *Stegocephala*, the episternum ("interclavicle") consists of a large bony plate, situated ventrally to the sternum, some of the various forms of which, as well as its relation to the pectoral arch and more particularly to the clavicles, will be seen by reference to Fig. 46.

The episternum of *Palæohatteria* and of recent *Lizards* and *Crocodiles* is essentially similar to that of the Stegocephala (Figs. 44, 46, and 47). In Lacerta and Crocodilus it arises, from before backwards, as a paired structure, which is not preformed in cartilage. An episternum is wanting in Chelonia and Ophidia, as well as in Chamæleo and Anguis.



FIG. 47.—PECTORAL ARCH OF PALÆOHATTERIA (from the ventral side)    After Credner.

*S*, scapula ; *C*, coracoid ; *Cl*, clavicle ; *Eps*, episternun.

In *Birds* no independent elements corresponding to this structure can be recognised ; the ligament extending between the clavicles and the sternal keel, the periosteal covering of the keel which is continued backward from this ligament, and the median portion of the fused clavicles when separately ossified ("interclavicle") may possibly have something to do with an episternum without being exactly homologous with it.

The origin and meaning of the mammalian episternum, which is preformed in cartilage, is not known; it has probably no direct connection with the similarly-named structure in Reptiles, but apparently agrees with the latter at any rate as regards position and relations in the embryo Mole (Fig. 47A).



FIG. 47A.—EPISTERNUM OF AN EMBRYO MOLE. (After A. Götte).

*St*, sternum ; *es*[1], central portion and *es*[2], lateral portion of the episternum ; *cl*, clavicle ; *r.c*, ribs. (The figure was constructed from two consecutive horizontal sections.)

In *Monotremes* (Fig. 48) and certain *Marsupials* a median and two lateral portions can be distinguished, the latter being in connection with the clavicles. In these Marsupials the median portion unites with the sternum, and as in Monotremes, becomes

ossified; while the lateral portions remain cartilaginous. In other Marsupials various stages in the reduction of the episternum are met with.

Amongst the *Placentalia* the episternum is retained in the most independent condition in certain South American Cavies as well as in the Porcupine and other Rodents in which it consists of a median and two lateral parts, which are, however, quite independent of one another, and are only connected by ligaments. The median,
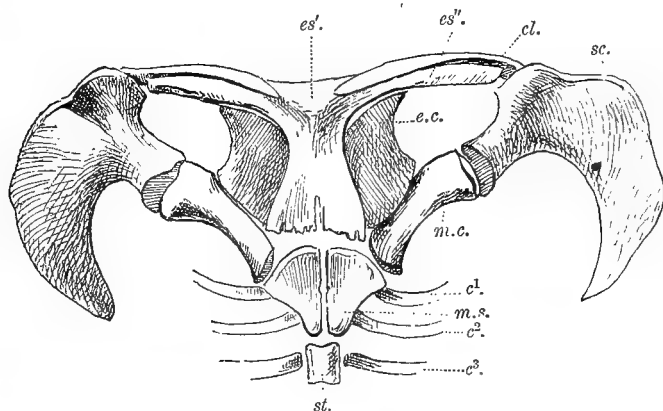


FIG.—48.—PECTORAL ARCH OF *Ornithorhynchus paradoxus.*

*m.s,* manubrium sterni ; $c^1$, $c^2$, $c^3$, first, second, and third ribs ; *st*, sternebra ; *sc*, scapula ; *m.c*, coracoid (metacoracoid) ; *e.c*, epicoracoid ; *cl*, clavicle ; $es^1$ nd $es^2$, episternum ("interclavicle").

cartilaginous portion is closely applied to the sternum, while the lateral portions are connected with the clavicles.

In the Sciuromorphæ and Myomorphæ the episternal apparatus is still further modified, the median piece having disappeared (or more probably having united with the sternum), while the small lateral pieces are attached to the manubrium and in the Sciuromorphæ articulate with the clavicles. In the Lagomorphæ fibro-cartilaginous lateral portions only are present, extending as far as the clavicles.


## V. THE SKULL.

### *Introduction.*

The question as to the primary origin of the skull in the Craniata has always taken a foremost place amongst the morphological problems relating to the structure of Vertebrates. Until past the middle of the present century the theory which held the field was the "*vertebral theory*" of Goethe and Oken, according to

which the skull consisted of a number of modified vertebræ
("cranial vertebræ"). On this theory, therefore, the skull was
regarded as a special modification of the anterior part of the
vertebral column, and a large number of facts were brought
forward in support of it : even when morphological science had
made further considerable advances, there still seemed to be a
certain amount of justification for it.

The arguments in support of the vertebral theory of the skull
may be briefly stated as follows. As in the vertebral column, three
stages may be distinguished in the skull, ontogenetically as well as
phylogenetically: viz., a *membranous*, a *cartilaginous*, and a *bony stage*
(comp. p. 36). There is thus an important correspondence between
these two parts of the cranio-spinal axis, and this is further em-
phasized by the fact that the notochord always extends for a certain
distance into the base of the skull, so that the latter is developed on
the same skeletogenous basis as, and in direct continuation of,
the vertebral axis.

This theory depended on giving an exact account merely of the
*skeletogenous elements* taking part in the formation of the skull,
and for a long time it was not recognised that this could not
possibly lead to a true interpretation of the origin of the verte-
brate head. To attempt to do so was to "put the cart before the
horse," by looking upon the *last acquisition of the head*—its *skeleton*
—as the leading point for future researches.

It was only very gradually ascertained that the skull has never
consisted of segmentally arranged cartilaginous portions, either in
the course of its ancestral history or in that of the development of
the individual. In the occipital region alone did it possibly at one
time possess distinct neural arches, owing to the assimilation of
more or fewer of the anterior segments of the trunk ; and the
view gradually gained ground that this important problem could
not be solved merely by an anatomical and embryological analysis
of the skeleton, but that a number of other parts and organs
which arise much earlier must also be taken into account
and their origin traced :—such are, the *sensory organs, brain* and
*cerebral nerves, cranial muscles,* and the *anterior part of the
alimentary canal* together with the *mouth* and *visceral clefts*.

A considerable advance was thus made, and the problem was
vigorously attacked both from the anatomical and embryological
sides ; and many of the researches which resulted have become
classical in the history of the subject. It is impossible here to
give more than the barest outlines of the results obtained, and
even now much remains to be elucidated in this complex question,
about many details of which numerous differences of opinion still
exist. Moreover, a knowledge of the development and distribu-
tion of the cerebral nerves is a necessary preliminary to the study
of cranial morphology : these are treated of in a subsequent
chapter, to which the reader is referred for explanation of parts of
the following paragraphs.

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The portion of the skull which is situated along the main axis in continuation of the vertebral column and which encloses the brain is known as the *brain-box* or *cranium*, and is primarily composed of cartilage. A series of cartilaginous arches arise in serial order on the ventral side of the brain-case; these encircle the anterior part of the alimentary tract like hoops, incomplete dorsally, and are distinguished from the cranial region as the *visceral* skeleton. The latter stands in important relation to branchial respiration, inasmuch as each consecutive pair of arches encloses a passage (gill-slit), communicating between the pharynx and the exterior; this is lined by endoderm, and through it the water passes in branchiate forms. The foremost visceral arch bounds the aperture of the mouth, thus forming a firm support for it, and giving rise to the skeleton of the *jaws*; the other arches function primarily as *gill-supports*. Both cranial and visceral portions may become ossified later.

Before the cartilaginous skeleton begins to be formed in the embryo, the greater part of the head consists of a soft, mesoblastic formative tissue, which gives rise to a membranous capsule around the brain: the individual cerebral nerves can already be plainly distinguished (*membranous stage*, comp. p. 36). The three *organs of the higher senses* also appear at a very early stage; and these, in the course of further development, come to be situated in definite bays or cavities within the head, and thus are of extreme importance in modifying the configuration of the skeletal structures which are formed around them later.

In the embryos of lower Vertebrates (*e.g.*, Elasmobranchs) more or less of the mesoblastic tissue which surrounds, isolates, and supports these organs becomes divided up metamerically into segments, so that a *segmentation into somites (protovertebræ)* occurs in the posterior part of the head as well as in the body (comp. pp. 8 and 36). The mesoblastic segments of the head, some of which enclose cavities arising from the cœlome (or the pre-oral gut), consist of a tissue from which later become differentiated all the *supporting structures*—including, of course, the skull, as well as the muscles (*myotomes*). Without going into further details as to the number and fate of these segments and their relation to the cerebral nerves, concerning which there is considerable diversity of opinion, it may be stated that the primary segmentation of the part of the head posterior to the auditory organ, in the region of the vagus and hypoglossal nerves, is at any rate more pronounced than that of the more anterior part of the head.

The relations of the visceral to the cranial skeleton, and those of both to the primary segmentation of the head, must also be taken into consideration. Both cranial and visceral regions must have been originally segmented, and each myotome at one time included a ventral portion (lateral plate of the mesoblast) which enclosed a corresponding section of the cranial cœlome, or

" head-cavity." Later, however, the visceral region became relatively shifted to a greater or less degree, especially in the anterior part of the head, so that its segments no longer corresponded to those of the cranial region. Thus we find that *the segmentation of the nervous, muscular, and visceral parts of the head do not correspond with one another.* But although the segmentation of the visceral portion of the skull has in the course of phylogeny reached a certain degree of independence, and the cranial portion alone can be looked upon as being made up of a series of somites, it must not be forgotten that mesoblastic tissue extends from the head-somites into the visceral arches, each of the two anterior of which still contain a cœlomic cavity at a certain period of development.

### *a.* **Brain-Case (Cranium).**

The first cartilaginous rudiments appear in the primitively membranous skull-tube in the form of a pair of rods, the *trabeculæ cranii.* These lie along the base of the brain, their posterior parts embracing the notochord ; they are thus divisible into *prochordal* (anterior) and *parachordal* (posterior) regions (Fig. 49), which may be continuous with one another. The parachordals soon unite to form a *basilar plate,* which grows round the notochord dorsally and ventrally, and thus early forms a solid support for the hinder part of the brain. The slender trabeculæ project forwards and enclose a space, which may be spoken of as the primitive pituitary space (Fig. 49).

These structures may undergo further development in many different ways in the various Vertebrate groups : the trabeculæ may become completely united with one another in the median line (Fig. 50, A), and the connective-tissue of the oral mucous membrane may become ossified to form a *parasphenoid* (B). In other cases, the trabeculæ may become compressed and partly aborted owing to the great development of the eyes : this obtains, *e.g.,* in certain Reptiles and in all Birds, in which a fibro-cartilaginous interorbital septum appears in their place (C).



FIG. 49.—FIRST CARTILAGINOUS RUDIMENTS OF THE SKULL.

*C,* notochord ; *PE',* separate parachordal elements ; *Tr,* trabeculæ cranii ; *PR,* pituitary space ; *N, A, O,* the three sense-capsules (olfactory, optic, and auditory).

In most cases a median cartilaginous bar *(intertrabecula)* is formed between the trabeculæ in front, fusing with them, and

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forming the ethmo-nasal septum (Fig. 51). It occasionally projects
forwards to form a rostrum (Figs. 55, 56, and 58).
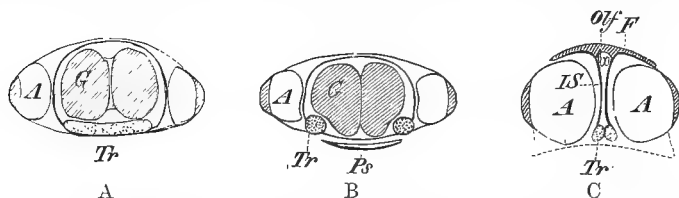


FIG. 50.—DIAGRAMMATIC TRANSVERSE SECTIONS OF THE HEAD IN EMBRYO—
(A) STURGEONS, ELASMOBRANCHS, ANURANS, AND MAMMALS ; (B) URODELES
AND SNAKES ; (C) CERTAIN TELEOSTEANS, LIZARDS, CROCODILES, CHELONIANS,
AND BIRDS.

*Tr*, trabeculæ cranii ; *G*, brain ; *A*, eyes ; *Ps*, parasphenoid ; *IS*, interobital
septum ; *F*, frontal ; *Olf*, olfactory nerve.

We must now further follow the processes of growth, start-
ing from the primary condition described above, in which
the trabeculæ have united together in
the middle line. The cartilaginous
basal plate now comes into relations
with the olfactory, optic, and auditory
organs (Fig. 51), around which carti-
laginous *capsules* are formed. Thus an
*olfactory*, an *orbital*, and an *auditory
region* are early differentiated.

The olfactory and auditory capsules,
especially in higher types, then become
more and more drawn in to the skull
proper, and the lateral edges of the
basal plate begin to grow upwards
round the brain on both sides, eventu-
ally extending even to the dorsal region.
Thus a continuous cartilaginous capsule
is formed, such as persists throughout
life in Elasmobranchs for example.
But in by far the greater number of
Vertebrates, the cartilage does not play
so great a part, and is, as a rule, con-
fined to the base and lower parts of
the sides of the skull and to the sense-
capsules, except in the occipital region,
where it always extends over the brain.
The rest of the skull, more particularly
the roof, becomes directly converted
from membrane into bone. At the
same time, bones may become differ-
entiated in connection with the primary



FIG. 51.—LATER STAGE IN THE
DEVELOPMENT OF THE PRIM-
ORDIAL SKULL.

*C*, notochord ; *B*, basilar plate ;
*Tr*, trabecula, which has
united with its fellow in
front of the pituitary space
to form the ethmo-nasal sep-
tum (*S*) ; *Ct*, cornu trabe-
culæ, and *AF*, antorbital
process, which support the
olfactory organ (*NK*) in
front and behind ; *Ol*, for-
amina for exit of the olfac-
tory nerves from the crani-
um ; *PF*, postorbital pro-
cess of trabecula ; *A*, eye ;
*O*, auditory organ.

cartilaginous skull (*chondrocranium*) itself, which is thus more or less completely replaced by an *osteocranium*. In general the higher the systematic position of the animal, the less extensive are the cartilaginous constituents and the more important the bony.

## *b.* **The Visceral Skeleton.**

The primarily cartilaginous visceral arches encircle the anterior section of the alimentary canal, lying embedded in the inner part of the walls of the throat (Figs. 52 and 53) and usually becoming ossified latter. They are always present in a greater number (up to as many as nine) in forms which possess gills than in higher types (Amniota), in which they gradually become reduced, and may undergo a change of function, certain of them in some cases taking on definite relations to the auditory organ and larynx.

The most anterior arch, serving as a support for the walls of the mouth and receiving its nerve supply from the trigeminal, arises first, and is distinguished from the other or *post-oral* arches as the *mandibular* arch. The post-oral arches only function as gill-bearers in the Anamnia : even the first of these, the *hyoid*, which is supplied by the facial nerve, becomes modified from those lying behind it: the latter, or *branchial arches* proper, are supplied by the glossopharyngeal and vagus. All the visceral arches must originally, however, have borne gills.



Fig. 52. — Diagrammatic Transverse Section of a still Later Stage in the Development of the Primordial Skull.

*C*, notochord ; *Tr*, trabeculæ, which enclose the brain (*C*) ventrally and laterally; *O*, auditory capsule ; *RH*, the cavity of the pharynx, enclosed by the visceral skeleton ; 1 to 4, the individual elements composing each visceral arch, which is united with its fellow by a basal piece (*Cp*).

Primarily unsegmented, the individual post-oral arches may become broken up into as many as four pieces, of which the uppermost becomes inserted under the base of the skull, while the lowermost is connected with its fellow by a median basal piece (Fig. 52).

The mandibular arch also undergoes segmentation, and becomes divided into a short proximal piece, the *quadrate,* and a long distal *mandibular* or *Meckel's cartilage* (Fig. 53). The quadrate grows out anteriorly into a process, the *palatoquadrate* or *palatopterygoid,* which usually becomes fixed to the base of the skull and forms the primary upper jaw, Meckel's cartilage forming the lower jaw.

The quadrate, which serves as a support (*suspensorium*) for the jaws, either remains separated from the skull by an articulation— that is, is only united to it by connective-tissue—or it forms one mass with it.

The hyoid—which has always close relations with the mandibular arch, and may also take part in its suspensorial apparatus [1]
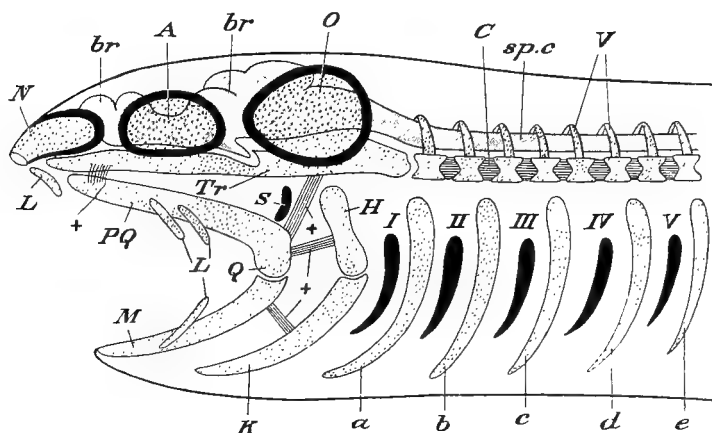


FIG. 53.—DIAGRAMMATIC FIGURE OF AN EMBRYONIC ELASMOBRANCH SKULL, SHOWING THE RELATIONS OF THE VISCERAL ARCHES.

*N*, nasal capsule ; *A*, eye ; *O*, auditory capsule ; *Tr*, trabecula ; *Q* and *PQ*, quadrate and palatopterygoid, which are bound to the trabecula by ligaments at † ; *M*, Meckel's cartilage ; *L*, labial cartilages ; *H*, hyomandibular ; *K*, hyoid arch ; *a* to *e*, branchial arches, between which the gill-clefts (*I* to *V*) are seen ; *S*, spiracle ; *C*, notochord ; *b*, vertebræ, *br*, brain ; *sp.c*, spinal cord.

—becomes divided, as do the true branchial arches, into a number of segments, the upper of which in many Fishes is distinguished as the *hyomandibular* (Fig. 53), from which a *symplectic* may be differentiated distally. In the mid-ventral line there is a basi-hyal connecting the arch of either side, and embedded in the tongue (*entoglossal* or *glossohyal*).

## *c.* **The Bones of the Skull.**

It is usual and convenient to distinguish in the entire skeleton between the bones which are formed in connection with cartilage, and eventually replace it to a greater or less extent (*cartilage*

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[1] It appears to be probable that the hyomandibular and hyoid proper are separate in origin : possibly also the *spiracular cartilage* (p. 75), often looked upon as representing fused mandibular rays, represents the remains of an entire arch ; and Dohrn maintains that Meckel's cartilage and the palatoquadrate each represents a distinct arch.

*bones*), and those which arise in connective-tissue, entirely inde-
pendent of cartilage (*membrane-* or *investing-bones*). But it must
be borne in mind that there is no hard and fast line between
these, and that histologically they are indistinguishable from one
. another. Bone is always phylogenetically formed *outside* the
cartilage, and its first appearance within cartilage (as in the
Amniota more particularly) is to be looked upon as a secondary
condition.[1] Again, in other cases (*e.g.*, in parts of the skeleton of
Elasmobranchs), true bones are not formed at all, there being
only a calcareous incrustation of the cartilage (calcified cartilage).

The bones arising in the membranous regions of the skull
(including the perichondrium) primarily come under the category
of the *dermal skeleton* and, as already mentioned with regard to
the latter, are to be looked upon as originating phylogenetically
in connection with dermal denticles (p. 30). In this manner
the bones of the mouth-cavity of Fishes and Amphibians, for
instance, still arise : it must be remembered that the epithelium
of the oral cavity is formed by invagination of the outer skin.

Such a mode of origin of the first skull-bones appears to be the
oldest and most primitive, and it is most apparent in the lower
Vertebrates (Fishes). This holds good also for those cases in which
bones are formed merely by deposition of calcareous matter directly
in the connective-tissue layer, without giving rise to tooth-struc-
tures (*e.g.*, all investing bones)—probably owing to an abbrevia-
tion of development.

The following lists give a summary of the most important
bones according to their different relations to the skull.

I. **Investing Bones of the Mouth-Cavity** (partly lying
within it, partly bounding it on the outer side).

1. Parasphenoid.
2. Vomer.
3. Premaxilla.
4. Maxilla.
5. Jugal.
6. Quadratojugal (in part).
7. Dentary.

[1] The different varieties of ossification may be conveniently classified as
follows :—
   I. "**Membrane Bones.**" (*a*) *Dermostoses*—ossifications of the dermis ; (*b*)
*parostoses*—ossifications of the looser subcutaneous tissue ; (*c*) *ectostoses*—ossifi-
cations of the inner layer of the fibrous investment (perichondrium) of a tract of
cartilage : these may extend into the latter, replacing it, and thus give rise
secondarily to
   II. "**Cartilage Bones**," (*endostoses*).
   It may, however, happen that in the course of generations an investing bone
may take the place of a cartilage bone, and the formation of cartilage be entirely
suppressed and not repeated again ontogenetically.

8. Splenial.
9. Angular.
10. Supra-angular.
11. Coronoid.
12. Palatine.
13. Pterygoid.

II. **Investing Bones of the Outer Surface** (enumerated from before backwards).

1. Nasal.
2. Lachrymal.
3. Frontal.
4. Prefrontal (of Reptiles).
5. Postfrontal or postorbital.
6. Supraorbital.
7. Parietal.
8. Temporal or squamosal.
9. Supraoccipital (in part).

III. " **Cartilage Bones**."

1. Basioccipital ⎫
2. Basisphenoid ⎬ Present only in Amniota (forming the base
3. Presphenoid ⎭    of the skull).
4. Exoccipital (and supraoccipital, in part).
5. Pro-, epi-, and opisthotic, also (in Teleostei) sphenotic and pterotic (forming the bony auditory capsule).
6. Orbito- ⎫ sphenoid, developed in the trabecular region.
7. Ali- ⎭
8. Ethmoid, together with the rest of the skeleton of the nose (turbinals, &c.).
9. Quadrate.
10. Articular.
11. Visceral skeleton (in part).

ANATOMY OF THE SKULL.

SPECIAL PART.

A. **Fishes.**[1]

In the **Cyclostomata**, the skull is developed essentially in the manner already described. Later, however, it shows many special peculiarities, probably in consequence of the suctorial (Petromyzon)

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[1] In Amphioxus (**Acrania**) there is no cranial skeleton, and the elastic non-cartilaginous rods which support the branchial apparatus are not comparable with the visceral skeleton of the Craniata.

or parasitic (Myxine) mode of life of these animals : the most important of these is the *absence of jaws* such as are present in all other Craniata; for this reason these forms are spoken of as *Cyclostomata* to distinguish them from the other craniate Vertebrates or **Gnathostomata**. Instead of the jaw-apparatus, which has doubtless become degenerated, and indications of which as well as of the hyoid can apparently still be seen (Fig. 54, *sb.oc.a*, *p. lat.c, sty.c, cn.c*), a number of cartilages are present supporting the anterior part of the head. In the adult Lamprey, for instance, the suctorial mouth is supported by various skeletal elements, amongst which may be mentioned a ring-like cartilage around the margin of the dome-shaped oral funnel, between the dorsal side
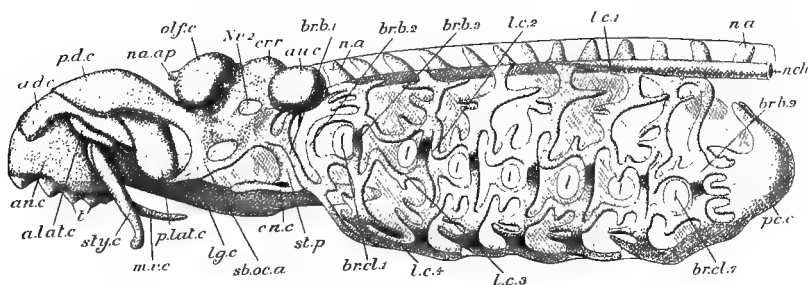


FIG. 54.—SKULL WITH BRANCHIAL BASKET OF *Petromyzon marinus.*
(After W. K. Parker.)

The cartilaginous parts are dotted. *a.d.c.* anterior dorsal cartilage ; *a.lat.c.* anterior lateral cartilage ; *an.c.* annular cartilage ; *au.c.* auditory capsule ; *br.b. 1—7*, vertical bars of branchial basket ; *br.cl. 1—7*, external branchial clefts ; *cn.c.* cornual cartilage ; *cr.r.* cranial roof ; *l.c. 1—4*, longitudinal bars of branchial basket ; *lg.c.* lingual cartilage ; *m.v.c.* median ventral cartilage ; *na.ap.* nasal aperture ; *nch.* notochord ; *Nv. 2*, foramen for optic nerve ; *olf.c.* olfactory capsule ; *pc.c.* pericardial cartilage ; *p.d.c.* posterior dorsal cartilage ; *p.lat.c.* posterior lateral cartilage ; *sb.oc.a.* sub-ocular arch ; *st.p.* styloid process ; *sty.c.* styliform cartilage ; *t.* teeth.

of which and the brain-case are a couple of large overlapping cartilages : the tongue is supported by a long, lingual cartilage. On the mucous membrane covering the annular and lingual cartilages inside the oral funnel are a number of *horny teeth*. The fibro-cartilaginous olfactory sac is *unpaired*, and opens on the *dorsal* surface of the head by a single nostril. The visceral skeleton also shows many exceptional peculiarities : it consists of a delicate cartilaginous basket-work (Fig. 54), and has a very superficial position ; we may accordingly speak of the unsegmented cartilages of which it is composed as "*extra-branchials*" to distinguish them from the true branchial arches of the Gnathostomata.

In Myxine, the extra-branchial basket-work is quite rudimentary and amongst other peculiarities, the long nasal passage is surrounded by cartilaginous rings, and communicates with the pharynx by a naso-palatine duct.

No fossil Cyclostomes are known, but *Palæospondylus gunni* from the Old Red Sandstone of Caithness possibly shows affinities with this group.

In the **Elasmobranchii** and **Holocephali** the skull presents the simplest conditions and most easily comprehensible relations, so that it may be taken as the starting-point for the study of the skull of all other Vertebrates. It consists of a simple carti-laginous and fibrous capsule either more or less immovably united with the vertebral column (Squalidæ,) or connected with it by articulations only (Raiidæ and Holocephali).
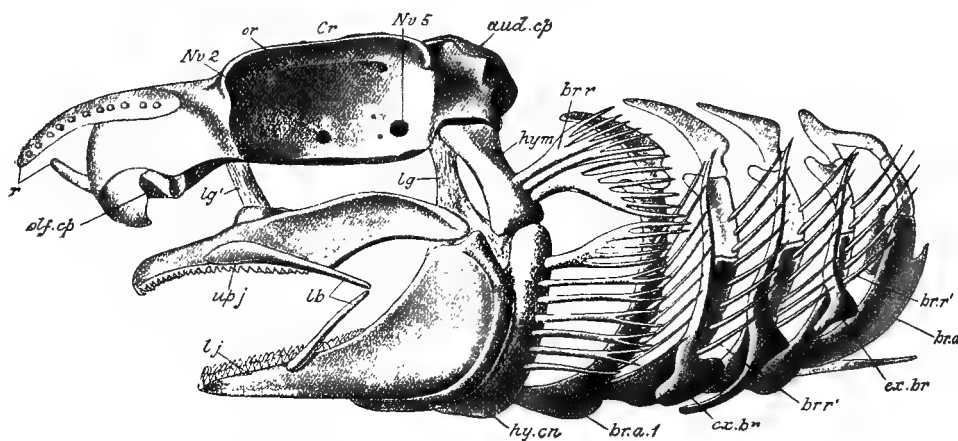


FIG. 55.—SKULL OF DOGFISH (*Scyllium canicula*). (From T. J. Parker's *Biology*, after W. K. Parker.)

*Cr.* cranium ; *aud.cp.* auditory capsule ; *or.* orbit ; *olf.cp.* olfactory capsule ; *r.* rostral cartilage ; *hy.m.* hyomandibular ; *up.j.* palatoquadrate ; *l.j.* Meckel's cartilage ; *hy.cn.* ventral part of hyoid arch ; *lg.lg'.* ligaments supporting the jaws from the cranium ; *lb.* labial cartilage ; *br.a. 1—5*, branchial arches ; *br.r, br.r'*, branchial rays arising from the hyoid and branchial arches ; *ex. br.* extra-branchial cartilages ; *Nv. 2*, optic foramen ; *Nv. 5*, foramen for trigeminal and facial nerves. (The spiracular cartilage is not indicated.)

True bones are never developed, the cartilage being merely calcified. In Elasmobranchs the palatoquadrate and lower jaw are provided with numerous teeth, arranged in rows ; in the Holocephali, the teeth have the form of strong and sharp-edged plates.

The nasal region is often elongated to form a long cut-water or rostrum (intertrabecula), at the proximal end of which the olfactory sacs are situated, their cavities being separated from the cranial cavity by a fibrous membrane ("lamina cribrosa"). Behind them are the deep orbital hollows, which are bounded posteriorly by the

strongly projecting auditory regions.  *Labial cartilages* are present
in connection with the lips, nostrils, and jaws (Figs. 55, 56, and 57).

The palatoquadrate is usually only united to the basis cranii by
ligaments, but in the Chimæroids (Fig. 57) it becomes immovably
fused with it, whence their name of Holocephali.   In the Sharks
and Rays the palatoquadrate is not directly united to the skull, but
is suspended from it by the *hyomandibular* (p. 70, Figs. 55 and 56).
In this case the skull may be described as *hyostylic*, to distinguish
it from *autostylic* skulls, in which the hyoid takes no part in
the suspensorium (Fig. 57).   A cleft, the *spiracle*, is situated in
front of the hyomandibular, and leads into the cavity of the mouth ;
on its anterior wall may be found remnants of the embryonic
spiracular gill, beneath which is a *spiracular cartilage* (comp. p. 70,
and Fig. 56).

The branchial skeleton is always well developed, and owing
to secondary segmentation and fusion of its parts exhibits char-
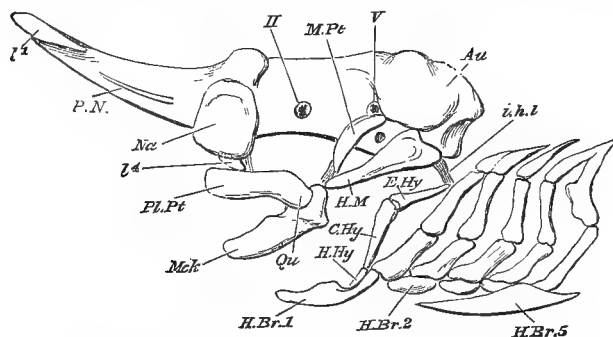


FIG. 56.—SKULL OF SKATE.   (After W. K. Parker.)

*Au*, auditory capsule ; *Na*, olfactory capsule ; *P.N*, prenasal rostrum ; *Pl.Pt*, *Qu*,
  palatoquadrate bar ; *Mck*, mandibular (Meckel's) cartilage ; *M.Pt*, spiracular
  cartilage ; *H.M*, hyomandibular ; *i.h.l*, interhyal ligament ; *E.Hy*, epihyal ;
  *C.Hy*, ceratohyal ; *H.Hy*, hypohyal ; *H.Br*, *1*, *2*, *5*, hypobranchials ; above
  them are seen the cerato-, epi-, and pharyngo-branchials ; *II*, optic foramen ;
  *V*, foramen for trigeminal and facial nerves.   (The branchial rays and extra-
  branchials are not indicated.)

acteristic modifications.   On the outer circumference of each
branchial arch, as well as on the hyomandibular and hyoid, radially-
arranged cartilaginous rays are situated, which serve as supports
for the gill-sacs (Fig. 55).   Externally to these rays small rod-like
" extra-branchial " cartilages are present.

In nearly all Elasmobranchs the gill-slits open freely on to
the surface of the body, but in Chlamydoselache and the Holo-
cephali a fold of skin arising from the hinder border of the
hyomandibular overlies them.   This is the first indication of a *gill-
cover* or *operculum*, such as is present in Teleosts and Ganoids.

Amongst the **Ganoids**, the lowest condition is met with in

those forms in which the hyaline primordial skull, immovably fixed to the vertebral column, is still retained (Fig. 58). These forms are spoken of as *Cartilaginous Ganoids*. As in Elasmobranchs, the cranial cavity reaches forwards to the ethmoidal region, but is separated from the latter by cartilage. The appearance of definite *bones*, however, divides them sharply off from the Elasmobranchs, and proves their skull to be at a much higher stage of development. These bones have the form of richly sculptured plates and shields, and are developed partly from the mucous membrane lining the mouth and covering the visceral skeleton, and partly from the skin covering the roof of the skull. In the first-named
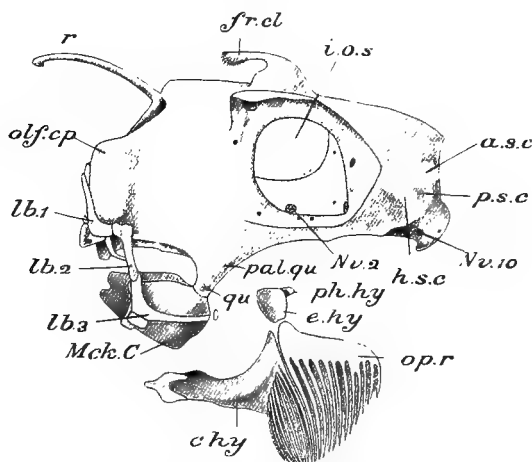


Fig. 57.—Skull of *Chimæra monstrosa*, Lateral View. (From Parker and Haswell's *Zoology*, after Hubrecht.)

*a.s.c.* position of anterior semicircular canal; *c.hy.* ceratohyal; *ep.hy.* epihyal; *fr.cl.* frontal clasper; *h.s.c.* position of horizontal semicircular canal; *i.o.s.* interorbital septum; *lb. 1, lb. 2, lb. 3,* labial cartilages; *Mck.C.* mandible; *Nv. 2,* optic foramen; *Nv. 10,* vagus foramen; *olf.cp.* olfactory capsule; *op.r.* opercular rays; *pal.qu.* palatoquadrate; *ph.hy.* pharyngohyal; *p.s.c.* position of posterior semicircular canal; *qu.* quadrate region; *r.* rostrum.

region a narrow parasphenoid forms a roof to the oral cavity and extends for some distance along the ventral side of the vertebral column. Ali- and orbito-sphenoids are present in the walls of the brain-case. The operculum is more pronounced than in the Holocephali, and is also supported by bones. The whole palato-mandibular apparatus, which is comparatively small and in connection with which bones are formed, is connected very loosely with the skull by means of a hyomandibular and symplectic, as well as by ligaments (Fig. 58).

The dermal skeleton attains a much more considerable develop-

ment in a second group of these Fishes—the *Bony Ganoids*—
and gives rise to a dense armour composed of numerous bones
lying on the roof and extending into all parts of the skull and
jaws (Fig. 59). The cartilage thus becomes reduced : it is, however,
largely retained in Amia. The opercular bones are more highly
developed than in cartilaginous Ganoids, and consist of an oper-
culum, a preoperculum, a suboperculum, and an interoperculum.

If all the membrane bones are removed and the cranium separated from
the vertebral elements which are fused with it, a surprising similarity will be
seen between the skull of Polypterus and that of Elasmobranchs—more par-
ticularly that of Chlamydoselache and Notidanus. On the other hand, the chon-
drocranium of Polypterus shows certain resemblances to that of the Amphibia.
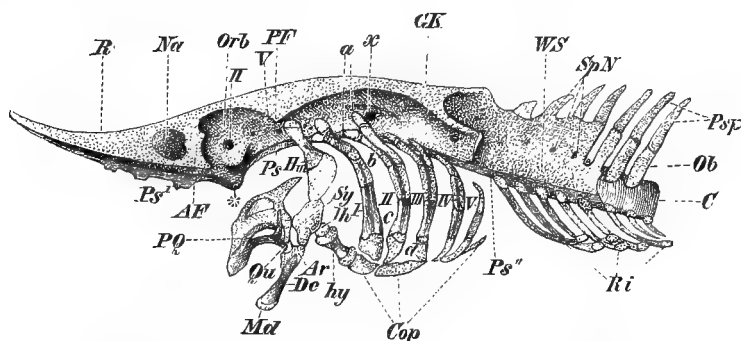


Fig. 58.—Cranial Skeleton of Sturgeon (*Acipenser*) after Removal of the
Exoskeletal Parts.

*WS*, vertebral column ; *SpN*, apertures for spinal nerves ; *Psp*, neural spines ;
*Ob*, neural arches ; *C*, notochord ; *GK*, auditory capsule ; *PF, AF,* postor-
bital and antorbital processes ; *Orb,* orbit ; *II,* optic foramen ; *x,* vagus
foramen ; *Na,* nasal cavity ; *R,* rostrum ; *,* prominent ridge on the basis
cranii ; *Ps, Ps¹, Ps″,* parasphenoid ; *PQ,* palatoquadrate ; *Qu,* quadrate ; *Md,*
mandible ; *De,* dentary ; *Ar,* articular ; *Hm,* hyomandibular ; *Sy,* symplectic ;
*Ih,* interhyal ; *hy,* hyoid ; *I* to *V,* first to fifth branchial arches, with their
segments—the double pharyngo-branchial (*a*), the epibranchial (*b*) the cerato-
branchial (*c*), and the hypobranchial (*d*) ; *Cop,* basal elements of the visceral
skeleton ; *Ri,* ribs.

The branchial skeleton in Ganoids consists of four or five more
or less strongly ossified gill-arches, decreasing in size antero-
posteriorly (Fig. 58) ; and in bony Ganoids the surface which looks
towards the throat is beset with teeth.

The Ganoidei are of special interest, as they, with the Elasmobranchii,
constitute the entire Fish-fauna through the Silurian, Devonian, and Carbo-
niferous periods, and as the Teleostei which appear later, are doubtless derived
from them. They also show connection with the Dipnoi and with the oldest
Amphibia from the Carboniferous and Trias (*Ganocephala, Stegocephala*).

In the **Teleostei**, the skull presents a large amount of varia-
tion ; its ground-plan, however, may always be derived from that

of the bony Ganoids, as is best seen by a comparison of the
Siluroids with Amia.   On the other hand, no relations with the
Amphibia are observable,
and we must consider the
whole group of the bony
Fishes as a side branch of
the piscine phylum.



FIG. 59.—SKULL OF *Polypterus bichir* FROM
THE DORSAL SIDE.

*Pmx*, premaxilla ; *Na*, external nostril ; *N*,
nasal; *Sb*, *Sb*[1], anterior and posterior
suborbital ; *Orb*, orbit ; *M*, maxilla ;
*Sp*, spiracular bones ; *PO*, preopercu-
lum (?) ; *SO*, suboperculum ; *Op*, oper-
culum ; *F*, frontal ; *P*, parietal ; *a*, *b*,
*c*, *d*, supraoccipital shields.   The two
arrows pointing downwards under the
spiracular shields show the position of
the openings of the spiracles on to the
outer surface of the skull.

Much of the cartilagin-
ous primordial skull persists
in most Teleostei ; the
cranial cavity may either
reach between the eyes as
far as the ethmoidal region,
or it may become narrowed
and arrested in the orbital
region (Fig. 50, C), in
which ali-, orbito-, and
basi-sphenoid ossifications
may occur (Fig. 61).   The
olfactory organs, as in most
other Fishes, consist of two
sacs lying in the cartilage of
the ethmoidal region.

The palatoquadrate bar
becomes differentiated into
a row of bony plates—
the quadrate, meso- and
metapterygoid, pterygoid,
and palatine.   The audi-
tory capsule ossifies from
five centres (see p. 72),
and in the occipital region,
as well as on the dor-
sal surface of the skull,
numerous bones are de-
veloped, for details of which
the reader is referred to
Figs. 60 and 61.

In many Teleosts a canal,
lying in the axis of the base of
the skull, encloses the eye-
muscles, and opens on either
side into the orbit.

All the bones bounding the oral cavity, viz., the vomer, the
parasphenoid, the premaxilla, and the maxilla, may bear teeth.
The maxilla, however, is usually edentulous, and both it and the

premaxilla vary much as to their development : the latter may even be absent.

Besides the above-mentioned bones in connection with the palatoquadrate bar, the cranial capsule of Teleosts is surrounded by other outworks consisting of bony plates and bars. These arise as true dermal bones in the region of the eyes (orbital ring), and in the gill-covers (opercular bones) : the latter are similar in number and name to those of bony Ganoids. A large number of
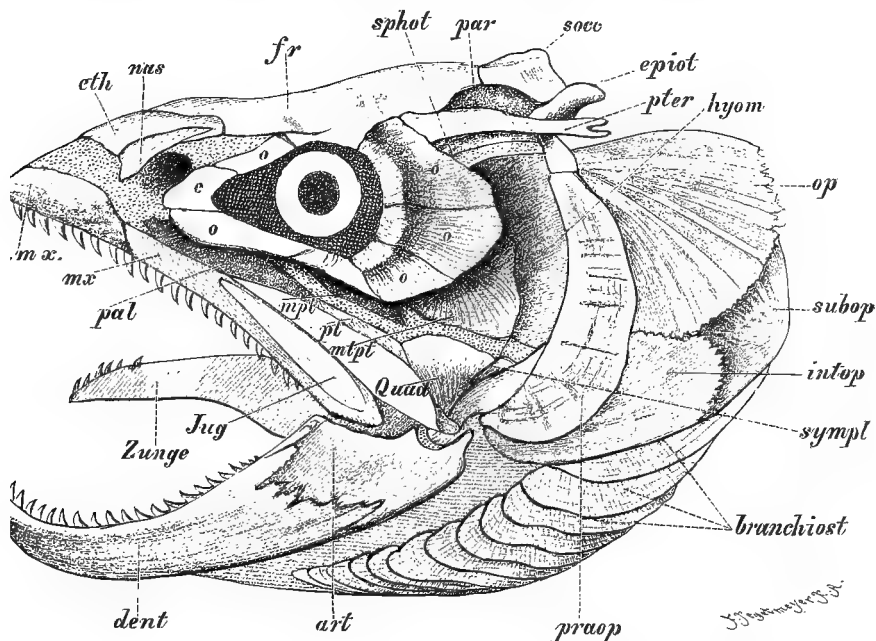


FIG. 60.—CRANIAL SKELETON OF THE SALMON. (From the left side.)

*Pmx*, premaxilla ; *eth*, supraethmoid ; *nas*, nasal ; *mx*, maxilla ; *jug*, jugal ; *pt*, pterygoid ; *mpt*, mesopterygoid ; *mtpt*, metapterygoid ; *Quad*, quadrate ; *hyom*, hyomandibular ; *pal*, palatine ; *fr*, frontal ; *o*, *o*, *o*, *o*, orbital ring ; *par*, parietal ; *sphot*, sphenotic ; *epiot*, epiotic ; *pter*, pterotic ; *socc*, supraoccipital ; *op*, operculum ; *praeop*, preoperculum ; *intop*, interoperculum ; *subop*, suboperculum ; *branchiost*, branchiostegal rays ; *dent*, dentary ; *art*, articular ; *Zunge*, tongue.

branchiostegal rays are developed in the ventral part of the opercular fold, or branchiostegal membrane (Fig. 60).

Anteriorly, the opercular apparatus lies against a bony chain consisting of three pieces—the hyomandibular, symplectic, and quadrate—which serves as a suspensorial apparatus for the lower jaw (Fig. 60). The latter consists of Meckel's cartilage and of several bony elements, the largest of which is the dentary :
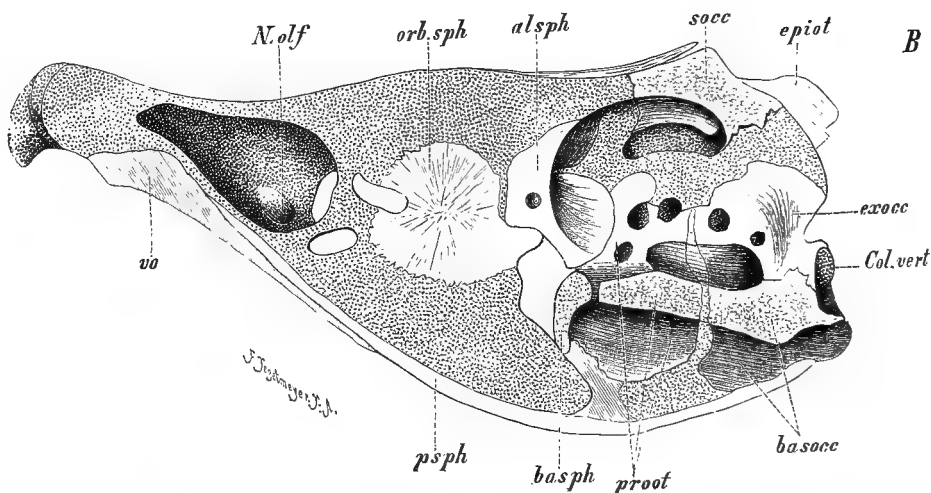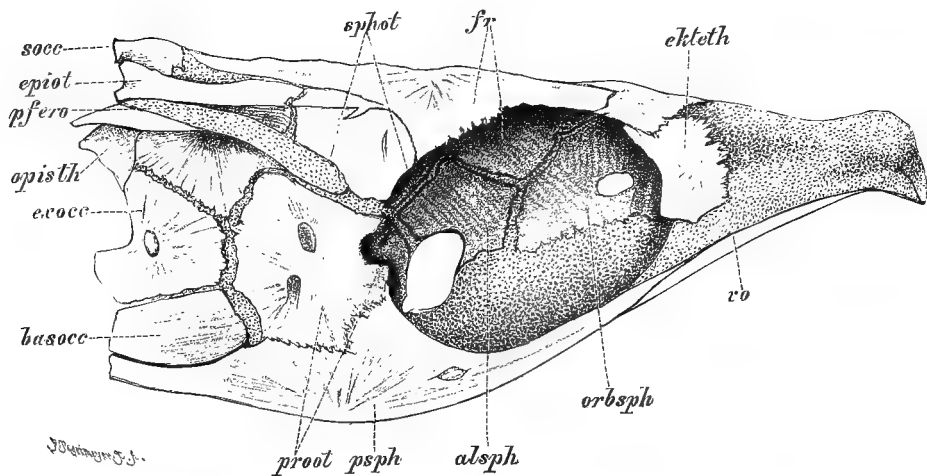
FIG. 61.—A. CRANIAL SKELETON OF SALMON AFTER REMOVAL OF THE JAWS,
    AND ORBITAL AND OPERCULAR BONES.  (From the right side.)
    B.   Longitudinal section of the same.   The cartilaginous parts are dotted.

*vo*, vomer ; *psph*, parasphenoid ; *fr*, frontal ; *ekteth*, ectoethmoid ; *socc*, supra-
occipital ; *exocc*, exoccipital ; *basocc*, basioccipital ; *Col. vert*, point of connec-
tion of the skull with the vertebral column ; *basph*, basisphenoid ; *orbsph*,
orbitosphenoid ; *alsph*, alisphenoid ; *epiot*, epiotic ; *pfero*, pterotic ; *opisth*,
opisthotic ; *proot*, prootic ; *sphot*, sphenotic ; *N.olf*, canal for the olfactory
nerve.

the others are, the articular, angular, and coronoid.   The last two,
however, may be wanting.

The hyoid arch is followed by four branchial arches and a
rudimentary fifth which forms the "inferior pharyngeal bone."

The dorsal segments of these arches become fused together to form the "superior pharyngeal bone," which, like the inferior pharyngeal, usually bears teeth.

A curious asymmetry is seen in the head of adult *Pleuronectidæ*. When hatched, these Fishes are quite symmetrical, but later on the eye of one side becomes rotated, so that eventually both eyes are situated on the same side ; in consequence of this, the skull also becomes asymmetrical.

The tactile barbules present on the head of many Fishes (*e.g.*, Siluroids) are supported by skeletal parts.

## B. **Dipnoi.**

The skull of the Dipnoi is in a sense intermediate between that of the Holocephali, Ganoidei, and Teleostei, on the one hand, and
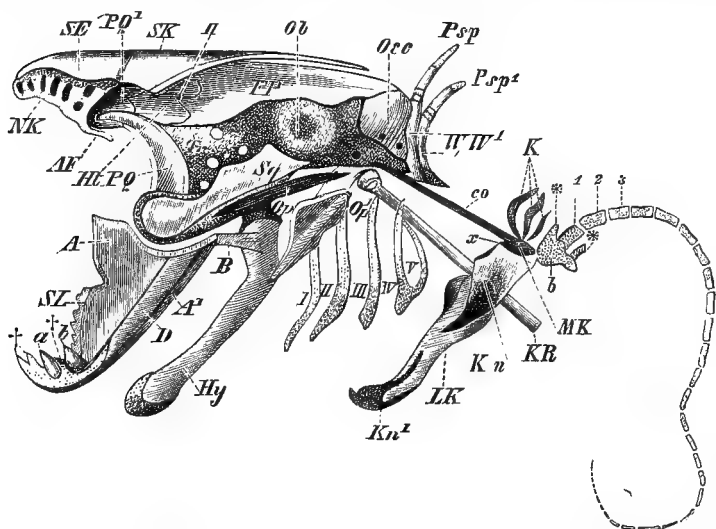


Fig. 62.—Cranial Skeleton, Pectoral Arch, and Anterior Extremity of *Protopterus*.

*W*, *W*¹, the vertebræ which are fused with the skull, with their neural spines (*Psp*, *Psp*¹) ; *Occ*, exoccipital, with the hypoglossal foramina ; *Ob*, auditorycapsule ; *Tr*, trabecular region, with the foramina for the trigeminal and facial nerves ; *FP*, fronto-parietal ; *Ht*, membranous fontanelle, perforated by the optic foramen (*II*) ; *SK*, supra-orbital ; *SE*, supra-ethmoid ; *NK*, cartilaginous nasal capsule ; *AF*, antorbital process (the labial cartilage, which has a similar position and direction, is not indicated) ; *PQ*, palatopterygoid, which converges towards its fellow of the other side at *PQ*¹ ; *Sq*, squamosal, covering the quadrate ; *A*, *A*¹, articular, joined to the hyoid (*Hy*) by a fibrous band (*B*) ; *D*, dentary ; ††, Meckel's cartilage, which is freely exposed, and grows out into prominences ; *SL*, *a*, *b*, teeth ; *Op*, *Op*¹, rudimentary opercular bones ; *I* to *V*, the five branchial arches ; *KR*, cranial rib ; *LK*, *MK*, lateral and median bony lamellæ which ensheathe the cartilage of the pectoral arch (*Kn*, *Kn*¹) ; *co*, fibrous band which binds the upper end of the pectoral arch with the skull ; *x*, articular head of the pectoral arch, with which the basal segment (*b*) of the free extremity articulates ; *,* *,* rudimentary lateral rays of the extremity (biserial type) ; 1, 2, 3, the three next segments of the free extremity ; *K*, external gills.

that of Amphibia on the other.  In certain respects, however, it presents special characters in which it differs from that of all these forms.

The chondrocranium is retained either entirely (Ceratodus) or at any rate to a large extent (Protopterus and Lepidosiren), and the cartilage bones are much less numerous than in Ganoids, exoccipitals only being present (Fig. 62).  The cranial cavity extends forwards between the orbits to the ethmoidal region, and the lamina cribrosa is largely cartilaginous.  The quadrate, which is covered by a *squamosal* (which corresponds to the preoperculum of Fishes), is fused with the cranium, and the connection between the latter and the strongly ossified palatopterygoid, which unites with its fellow anteriorly, is a very close one.

The lattice-like cartilaginous nasal capsules are situated right and left of the apex of the snout, close under the skin.  As in all the higher Vertebrates, each nasal cavity communicates with the mouth by *internal nostrils* (*choanæ*) as well as with the exterior by the external nostrils, which are, however, covered by the upper lip.  The labial cartilages are directly connected with the internasal septum.

The occipital region is immovably connected with the vertebral column, some of the anterior vertebræ being firmly united with the skull.  The teeth, which are sharp and blade-like, are covered with enamel, and are borne on the palatopterygoid and mandible; small "vomerine teeth" are also present, though there is no vomer.  The gill-covers and branchiostegal rays are greatly reduced, and even the five cartilaginous gill-arches are in a very rudimentary condition in Protopterus and Lepidosiren.

The strong lower jaw is ossified by an articular, a dentary, an angular, and a splenial, on the last mentioned of which the teeth are borne; Meckel's cartilage extends for a short distance anteriorly to the dentary.

The Dipnoi are an extremely ancient group ; they existed in the Trias and Carboniferous periods, and possibly even extended into the Silurian.  Several facts as regards their skull cannot be satisfactorily elucidated until something is known of its development.  The morphology of the so-called "cranial rib" (Fig. 62), for instance, is not at present understood.

## C. **Amphibia.**

**Urodela.**—The comparatively simple skull of tailed Amphibians is distinguished from that of bony Fishes in general principally by negative characters,—on the one hand by the presence of less cartilage in the adult, and on the other by a reduction in the number of bones.  In the larval condition (Fig. 63), the chondrocranium, with its nasal, orbital, and auditory
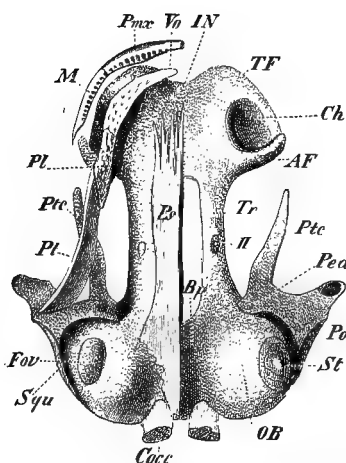
FIG. 63.—SKULL OF A YOUNG AXOLOTL. Ventral view.
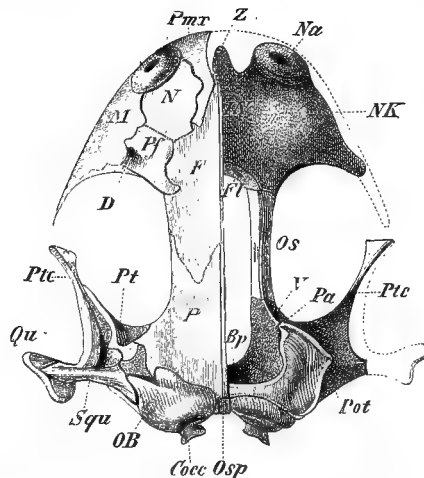


FIG. 64.—SKULL OF *Salamandra atra* (ADULT). Dorsal view.
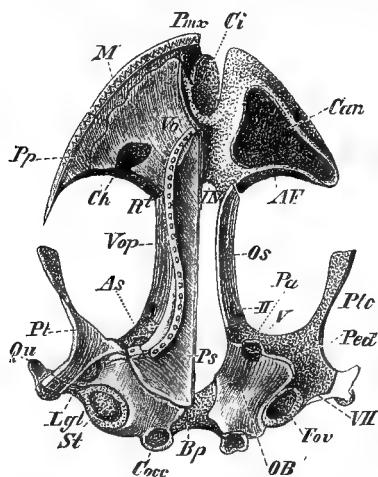


FIG. 65.—SKULL OF *Salamandra atra* (ADULT). Ventral view.

*Tr*, trabecula ; *OB*, auditory capsule ; *Fov*, fenestra ovalis, closed on one side by the stapes (*St*) ; *Lgt*, ligament between the stapes and suspensorium ; *Cocc*, occipital condyles ; *Bp*, cartilaginous basilar plate between the auditory capsules ; *Osp*, dorsal tract of the occipital cartilage ; *IN*, internasal plate, which extends laterally to form processes (*TF* and *AF*) bounding the internal nostrils (*Ch*) ; *NK*, nasal capsule ; *Can*, nasal cavity ; *Na*, external nostrils ; *Fl*, foramen for the olfactory nerve ; *Z*, tongue-like outgrowth (intertrabecula) of the internasal plate, which forms a roof for the internasal cavity ; *Qu*, quadrate ; *Ptc*, cartilaginous pterygoid ; *Pot*, otic process, *Ped*, pedicle, and *Pa*, ascending process, of the quadrate ; *Ps*, parasphenoid ; *Pt*, bony pterygoid ; *Vo*, vomer ; *Pl*, palatine ; *Pp*, palatine process of maxilla ; *Vop*, vomero-palatine ; *Pmx*, premaxilla ; *M*, maxilla ; *Os*, sphenethmoid ; *As*, prootic ; *N*, nasal ; *Pf*, prefrontal, perforated at *D* for the lachrymal duct ; *F*, frontal ; *P*, parietal ; *Squ*, squamosal ("paraquadrate," Gaupp) ; *II*, optic, *V*, trigeminal, and *VII*, facial foramina ; *Rt*, point of entrance of the ophthalmic branch of the fifth nerve into the nasal capsule.

regions, has very distinctly the relations described in the introduction to this chapter. The auditory capsules (Figs. 63 to 65)—which are bound together by cartilaginous tracts in the basi- and supra-occipital regions, and generally become strongly ossified later by the exoccipitals and prootics,—show a new and important modification as compared with those of Fishes in the presence of an aperture, the *fenestra ovalis*, on the outer and lower side of each. This fenestra is closed by a cartilaginous plug, the *stapedial plate*, probably corresponding to a part of the wall of the auditory capsule; from it a rod-like cartilage or bone, the *columella auris*, corresponding phylogenetically to the upper element of the hyoid arch, extends outwards towards the quadrate in most Urodeles and serves to conduct the sound to the inner ear, the position of the semicircular canals of which is indicated by corresponding cartilaginous ridges on the capsule.

In all Amphibians two condyles for articulation with the first vertebra are developed on the ventral periphery of the foramen
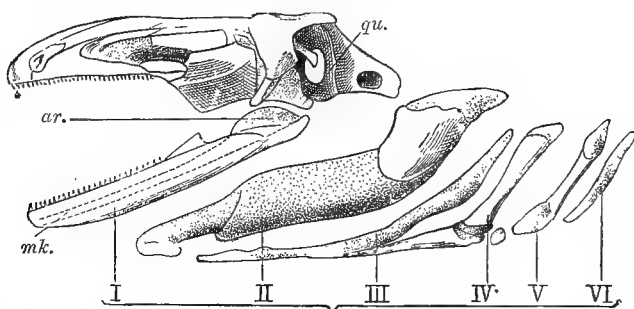


FIG. 66.—SKULL AND VISCERAL ARCHES OF *Menopoma*. (From the side.)

I, mandible; II, hyoid; III–VI, branchial arches; *qu*, quadrate, above which is the squamosal; *ar*, articular; *mk*, Meckel's cartilage, enclosed by the dentary bone.

magnum. The occipital region is ossified by two exoccipitals, a bony supra- and basioccipital rarely being present in recent forms (certain Anura).

The large nasal capsules, consisting throughout life of considerable cartilaginous portions, are connected with the auditory capsules by means of the trabeculæ, which give rise to the side walls of the skull and become more or less entirely ossified as the sphenethmoid and prootics. The cranial cavity is closed dorsally by the frontals and parietals, and ventrally by the parasphenoid, which is sometimes provided with teeth. In front of it are the vomers, which bound the internal nostrils; in adults each vomer becomes fused with the corresponding palatine, which forms a delicate bar lying on the ventral surface of the

parasphenoid.    These relations are secondary, for in the larval
condition a typical palatoquadrate or pterygopalatine bar is present
(Fig. 63).    The lamina cribrosa (p. 74) is either cartilaginous (*e.g.*,
Salamandra) or membranous (*e.g.*, Triton); or the cranial cavity
may be closed in front by special modifications of the frontals.

On the outer side of the vomer lies the maxilla, and in front of
this is a premaxilla which usually encloses, or at least bounds, a
cavity.    The latter bone extends on to the dorsal surface of the
skull and abuts against the nasal, behind which usually follows a
prefrontal.

The suspensorium is much more simple than that of Fishes
(Figs. 63—66).    It consists of the quadrate only, which has
usually four typical processes connecting it with surrounding parts.
and which becomes fused secondarily with the skull.    On the
outer surface of the quadrate an investing bone, the squamosal,[1]
becomes developed.

In Tylototriton verrucosus the quadrate sends forwards a process which
connects it with the maxilla : this is quite exceptional amongst Urodeles.

With the exception of the lower jaw, in connection with which
articular, splenial, and dentary bones are developed, the visceral
skeleton of Urodeles undergoes various modifications in the different
types.    We may consider the ground-form, as exhibited in the larva,
to consist of five pairs of bars in addition to the mandibular arch
(Fig. 66).    The anterior bar, or hyoid, consists of two segments (Fig.
67, A), as do also the two first branchial arches.    The third and
fourth branchial arches are much smaller, and each is composed of
a single segment.    All the above-named arches are connected
with their fellows of the other side by means of a single or double
basal piece.    At the close of larval life, that is, when the gills are
lost, the two hinder pairs of arches disappear entirely, while the
two anterior pairs undergo changes as regards form and position,
and may become more or less densely ossified (Fig. 67, B—D).

In the genus Spelerpes, which possesses a sling-like tongue, the dorsal
segment of the first branchial arch grows out into a long cartilaginous fila-
ment, which extends far back under the dorsal integument (Fig. 67, D).

The skull of the *Gymnophiona* differs from that of Urodeles mainly in its
extremely solid and strong character, the ossifications being more extensive.

In the extinct tailed Amphibians (*i.e.*, *Stegocephala*, Fig. 68) some of which
were comparatively gigantic, the cranial bones were very numerous and dense.
A *parietal foramen* was present, as well as a ring of orbital bones.    These
forms possessed the same number of visceral arches as Urodeles, and it has
been shown that they (*e.g.*, *Branchiosaurus*) underwent a metamorphosis.
Existing Amphibia cannot have been derived directly from them.

**Anura.**—The skull of the tailless Batrachia is at first sight
very similar to that of Urodeles.    It undergoes, however, an

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[1] According to Gaupp, a true squamosal is never present in existing Amphibia,
and the bone which is usually so designated he calls the *paraquadrate*.

essentially different and much more complicated development, and cannot in any way be directly derived from that of tailed Amphibians.
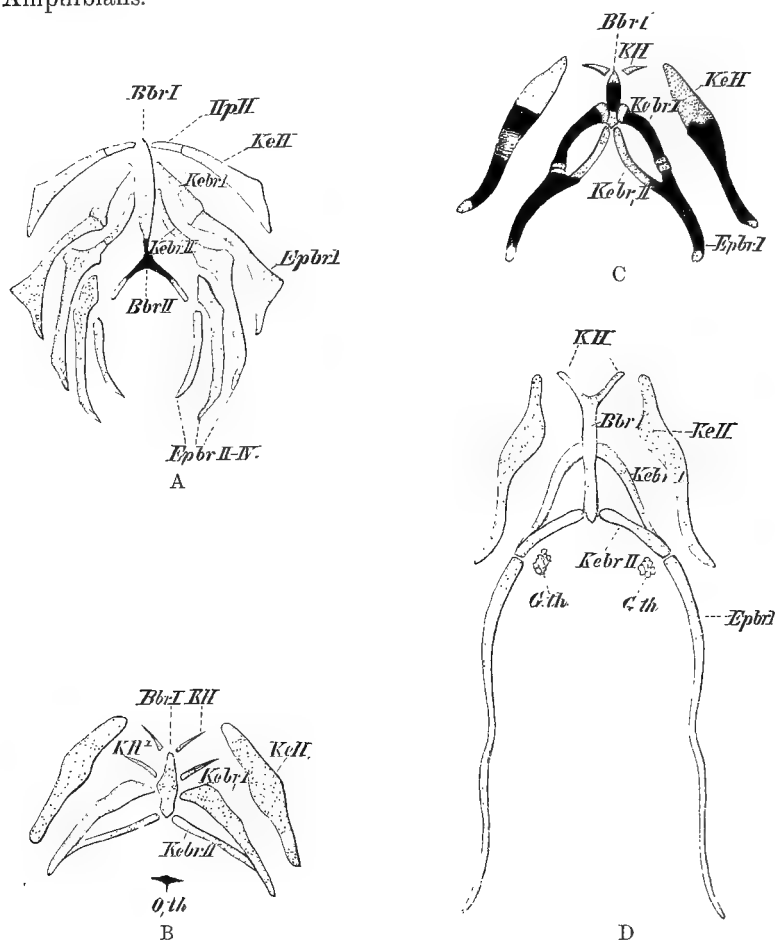


FIG. 67.—HYOBRANCHIAL APPARATUS OF URODELES.    A, Axolotl (*Siredon* stage of *Amblystoma*); B, *Salamandra maculosa;* C, *Triton cristatus;* D, *Spelerpes fuscus.*

*Bbr, I, II,* first and second basibranchial; *KeH,* ceratohyal; *HpH,* hypohyal; *Kebr I, II,* first and second ceratobranchial; *Epbr I* to *IV,* first to fourth epibranchial; *KH, KH¹,* small anterior and posterior pairs of cornua; *O.th,* part of skeleton of larynx; *G.th,* thyroid gland.

A *suctorial mouth,* provided with labial cartilages and horny jaws, is present in the larva.    An advance on Urodeles is seen in the formation of a *tympanic cavity* which is closed externally by a tympanic membrane, while internally it opens into the mouth by an

*Eustachian aperture.* With the exception of certain small regions (fenestræ) on the dorsal side, the skull of Anura forms a com-
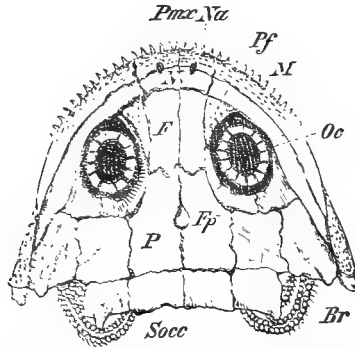


FIG. 68.—RESTORATION OF THE SKULL OF A STEGOCEPHALAN (from the Carboniferous of Bohemia). (After Fritsch.)

*Pmx*, premaxilla ; *M*, maxilla ; *N*, nasal ; *Na*, nostril ; *F*, frontal ; *Pf*, prefrontal ; *P*, parietal ; *Fp*, parietal foramen ; *Socc*, supraoccipital ; *Br*, branchial apparatus : *Oc*, sclerotic ring (orbital bones.)

plete cartilaginous box, the ethmoid region being at first entirely cartilaginous, and later becoming ossified by a sphenethmoid, which
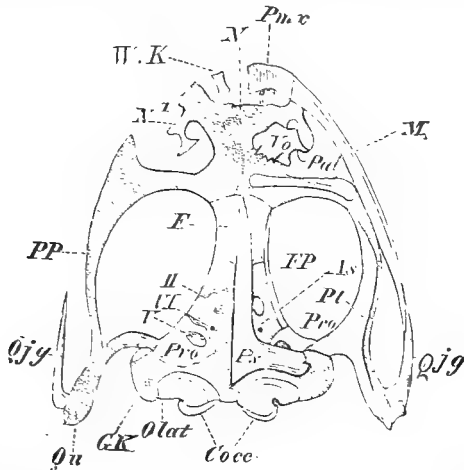


FIG. 69.—SKULL OF *Rana esculenta*. Ventral view. (After Ecker.)

The investing bones are removed on the right side.

*Cocc*, occipital condyles ; *Olat*, exoccipital ; *GK*, auditory capsule ; *Qu*, quadrate ; *Qju*, quadratojugal ; *Pro*, prootic ; *Ps*, parasphenoid ; *As*, alisphenoid region ; *Pt*, bony pterygoid ; *PP*, palatopterygoid ; *FP*, frontoparietal ; *E*, sphenethmoid girdle bone) ; *Pal*, palatine ; *Vo*, vomer ; *M*, maxilla ; *Pmx*, premaxilla ; *N*, *N*, cartilages in connection with the nasal capsules ; *W.K*, prorhinal cartilage ; *II*, *V*, *VI*, foramina for optic, trigeminal, and abducent nerves.

encircles the whole skull in this region and is perforated by the
olfactory nerves.

In the adult the bones are not so numerous as in Urodeles, and
the frontal and parietal of either side as a rule fuse together, thus
giving rise to a fronto-parietal. The maxillary bar grows back-
wards much further than in Urodeles, and becomes connected with
the suspensorium by means of a small intermediate bone, the quad-
ratojugal (Fig. 69). The maxillary arch is therefore complete, as
in Tylototriton amongst
Urodeles (p. 85). The
palatoquadrate is united
anteriorly with the carti-
laginous nasal capsule.
(For the relations of
the bones bounding the
mouth-cavity compare
Fig. 69.) The bones of the
lower jaw are a dentary
and an angular, the distal
end of Meckel's cartil-
age ossifying as a small
" mentomeckelian."

There is a much
greater reduction of the
branchial skeleton at the
close of larval life than
in Urodeles. In the
larva representatives of
the hyoid and of four
branchial arches can be
recognised, but these are
all fused together and
form a continuous struc-
ture, reminding one of
the branchial basket-
work of the Lamprey.
In the adult this be-
comes greatly reduced,
and the apparatus con-



FIG. 70.—HYOBRANCHIAL SKELETON OF LARVAL
(A) AND ADULT (B) FROG.
(After Gaupp.)
*bs*, body of the hyoid ; *a.c*, anterior cornua ;
*p.c*, posterior cornua.

sists of a broad cartilaginous plate in the floor of the mouth, with
long anterior and shorter posterior (thyro-hyal) cornua, the latter
of which become ossified.

### D. Reptiles.

Although as regards the structure of the skull existing Reptiles
and Amphibians are widely separated from one another, certain
resemblances exist between their extinct representatives (*e.g.*,
Palæohatteria and the Stegocephala).

Excepting in the naso-ethmoidal region, the whole chondro-cranium usually becomes almost obliterated by an extensive process
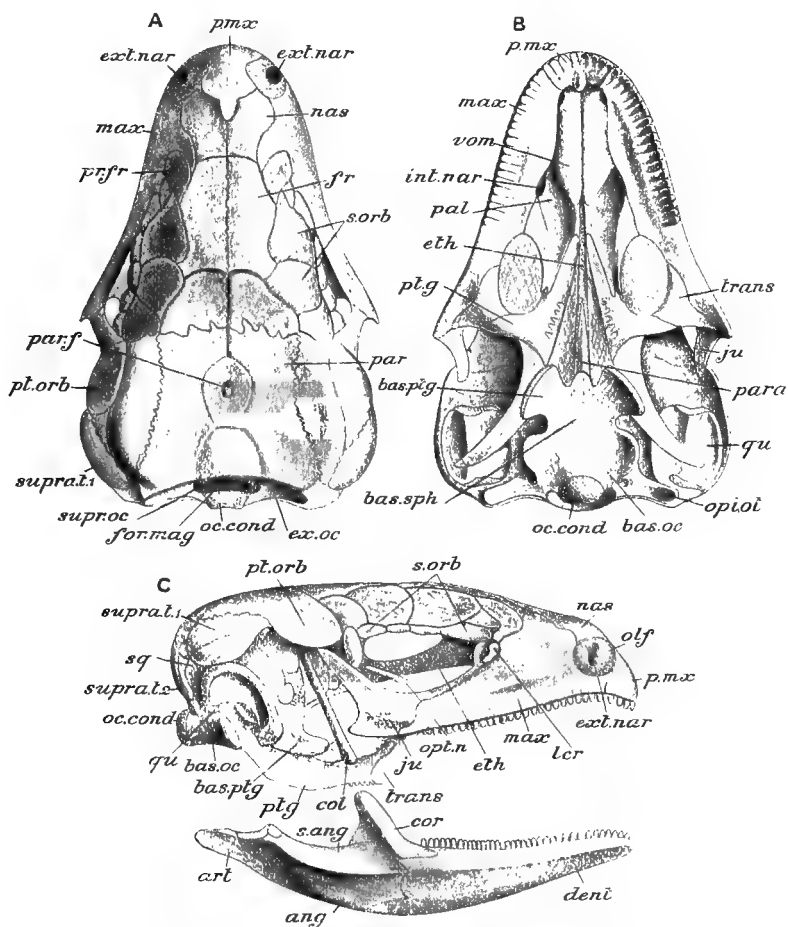


FIG. 71.—SKULL OF *Lacerta agilis* (from Parker and Haswell's *Zoology*, after W. K. Parker).

A, from above ; B, from below ; C, from the side. *ang*, angular ; *art*, articular ; *bas.oc*, basioccipital ; *bas.ptg*, basipterygoid processes ; *bas.sph*, basi-sphenoid ; *col*, epipterygoid ; *cor*, coronary ; *dent*, dentary ; *eth*, ethmoid ; *ex.oc*, exoccipital ; *ext.nar*, external nares ; *for.mag*, foramen magnum ; *fr*, frontal ; *int.nar*, internal nares ; *ju*, jugal ; *lcr*, lachrymal ; *max*, maxilla ; *nas*, nasal ; *oc.cond*, occipital condyle ; *olf*, olfactory capsule ; *opi.ot*, opis-thotic ; *opt.n*, optic nerve ; *pal*, palatine ; *par*, parietal ; *para*, para-sphenoid ; *par.f*, parietal foramen ; *p.mx*, premaxillæ ; *pr.fr*, prefrontal ; *ptg*, pterygoid ; *pt.orb*, postorbital ; *qu*, quadrate ; *s.ang*, supra-angular ; *s.orb*, supraorbitals ; *sq*, squamosal ; *supra.t.1*, *supra.t.2*, supratemporals ("paraquadrate," Gaupp) ; *trans*, transverse bone ; *supra.oc*, supraoccipital ; *vom*, vomer.

of ossification, which gives the skull a very firm and solid appearance; only amongst Lizards (Fig. 71), and especially in Hatteria is the cartilage retained to any considerable extent, and owing to the conformation of the bones in the posterior region, the skull in these forms presents a number of distinct spaces or fossæ in the dry state.

In Snakes and Amphisbænians the cranial cavity extends forwards between the orbits as far as the ethmoidal region, while in the Lacertilia, Chelonia, and Crocodilia—in which a fibro-cartilaginous interorbital septum perforated by the olfactory nerve is present—its anterior boundary is much further back.

The parasphenoid, which plays so important a part as an investing bone of the roof of the mouth in Fishes and Amphibians,
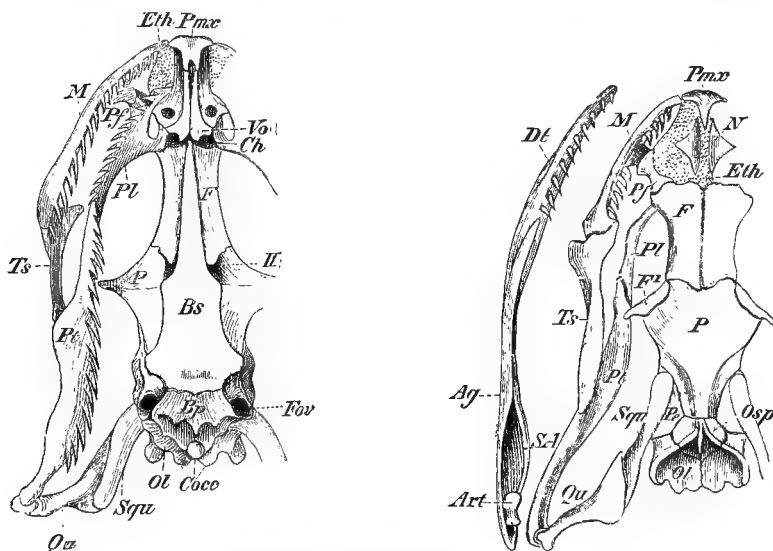


FIG. 72.—SKULL OF SNAKE (*Tropidonotus natrix*), dorsal view.
FIG. 73.— ,, ,, ,, ,, ventral view.

*Cocc*, occipital condyle; *Osp*, supraoccipital; *Ol*, exoccipital; *For*, fenestra ovalis; *Pe*, periotic; *P*, parietal; *F*, frontal; $F^1$, postfrontal; *Pf*, prefrontal; *Eth*, ethmoid; *N*, nasal; *Pmx*, premaxilla; *M*, maxilla; *Bp*, basioccipital; *Bs*, basisphenoid; *Ch*, posterior nostrils; *Vo*, vomer; *Pl*, palatine; *Pt*, pterygoid; *Ts*, transverse bone; *Qu*, quadrate; *Squ*, squamosal; *Art*, articular; *Ag*, angular; *SA*, supra-angular; *Dt*, dentary; *II*, optic foramen.

begins to disappear; amongst Reptiles it only attains any important development in Snakes, where the anterior part remains and forms the base of the interorbital region. Its place is taken by two cartilage bones, the *basioccipital* and *basisphenoid*, situated along the basis cranii. In contradistinction to the Amphibia, only a *single* condyle connects the skull with the vertebral column: this, on close examination, is seen to be formed of three parts, derived from the basioccipital and exoccipitals respectively.

The roofing bones of the skull are well-developed and in the Lacertilia may become closely united with overlying dermal bones, while the trabecular region (*ali*- and *orbitosphenoids*) becomes of secondary importance in the adult, its place being partly taken by processes growing downwards from the frontal and parietal : this is especially the case in Snakes.

The parietals are paired in the Chelonia and in Hatteria ; in all other Reptiles they become fused together, as do also the frontals in many Lizards and Crocodiles. A *parietal foramen*[1] is present in many Lizards.

The topographical relations of the several bones to one another are shown in Figs. 71 to 74. It will be seen in them that the ground-plan of the Urodele skull is here fundamentally retained. In addition, however, to a postorbital, an imperfect circumorbital ring of bones is present in Lizards. In many Lizards, moreover,
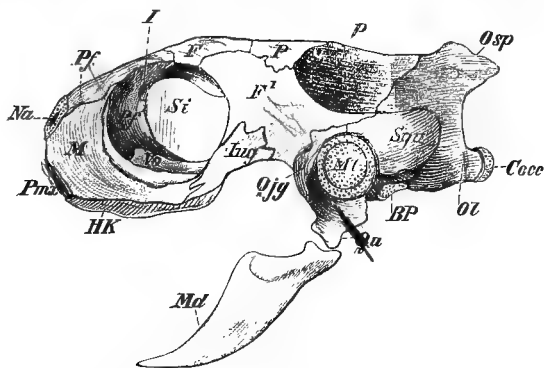


FIG. 74.—SKULL OF YOUNG WATER-TORTOISE (*Emys europaea*). Side view.

*O.p*, supraoccipital, which gives rise to a crest ; *Pf*, prefrontal, which forms a great part of the anterior boundary of the orbit ; *I*, point of entrance of the olfactory nerve into the nasal capsule ; *Na*, external nostril ; *Si*, interorbital septum ; *HK*, horny sheaths of jaws ; *Iug*, jugal ; *Qjg*, quadratojugal ("para-quadrate," Gaupp) ; *Mt*, tympanic membrane ; *BP*, cartilaginous interval between basioccipital and basisphenoid ; *Md*, mandible. Other letters as in Figs. 72 and 73.

a rod-like bone, the *epipterygoid* (also represented in Crocodiles), connects the parietal with the pterygoid, and a *transverse bone* extending from the maxilla to the pterygoid is typically present in Reptiles, but is wanting in the Chelonia and Typhlopidæ.

The auditory capsules are ossified from three centres, the prootic usually remaining free, and the epiotic uniting with the supraoccipital and the opisthotic with the exoccipital. A *fenestra rotunda* is present in its walls in addition to a fenestra ovalis, into which latter the stapedial plate of the columella is inserted (see p. 84), and the tympanic cavity in most Reptiles communicates with the pharynx by means of an Eustachian tube.

[1] In certain Chameleons its representative is in the *frontal*.

The columella here also probably arises in connection with the upper end of the hyoid arch (see p. 84), with which it is continuous in Hatteria.

The quadrate alone forms as the suspensorium for the lower jaw: it may be articulated with the skull (Ophidia,[1] most Lacertilia) or firmly fixed to it (Hatteria, Chelonia, Crocodilia).

According to Gaupp, a squamosal is wanting in narrow-mouthed Snakes and Hatteria, and a *paraquadrate*, comparable to that of the Amphibia (p. 85) is present in almost all Lizards and Chelonians, a quadratojugal being found only in Hatteria.

The pterygopalatine arch is well developed in all Reptiles. In Snakes and Lizards it is more or less movable and free from the base of the skull, while in Chelonians and Crocodiles it meets with its fellow to a greater or less extent in the middle line, and shelf-like palatine processes of the maxilla also come into connection with the palatines :—thus a secondary roof is formed to the mouth-cavity distinct from the true (sphenoidal) base of the skull. The cavity thus formed closes in the posterior prolongation of the nasal chambers, which consequently become sharply differentiated from the mouth. In Chelonians the pterygoid bones do not take part in the formation of this *hard palate*, which in Crocodiles is much more markedly developed, and is formed by the premaxillæ, maxillæ, palatines, and pterygoids, the posterior nostrils here opening far back into the pharynx (Fig. 75).



FIG. 75.—SKULL OF A YOUNG CROCODILE. (Ventral view.)

*Cocc*, occipital condyles; *Ob*, basioccipital; *Ch*, internal nostrils; *Pt*, pterygoid; *Orb*, orbit; *Pl*, palatine; *M*, palatine process of maxilla; *Pmx*, premaxilla; *Ts*, transverse bone; *Jg*, jugal; *Qj*, quadratojugal ("paraquadrate," Gaupp); *Qu*, quadrate.

A number of bones arise in connection with the lower jaw, viz., a dentary, angular, supra-angular, splenial, coronoid, and articular.

Teeth are well developed in all Reptiles except Chelonians,

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[1] In Snakes (Figs. 72 and 73) (except Tortrix), the quadrate is only indirectly connected with the skull by means of the squamosal, which extends backwards, and thus throws the articulation of the lower jaw far back, giving rise to a very wide gape. In most Snakes, and particularly in the Viperine forms, the facial bones are capable of movement upon one another, but in Typhlops they are immovably connected with the skull. The two rami of the mandible are connected by a more or less elastic ligament.

in which they are replaced functionally by strong horny sheaths on the edges of the jaws. The teeth may be borne on the palatine and pterygoid, as well as on the maxilla, premaxilla (which is usually unpaired), and dentary.

In the young Hatteria only amongst existing Reptiles do the vomers bear teeth (usually one on each). In certain fossil forms brush-like masses of sphenoidal teeth were present.

The remarkable horned skull of the gigantic *Ceratopsidæ* (Dinosauria) which reached a length of nearly seven feet, possessed horny beaks in addition to teeth on the maxilla and dentary. A parietal foramen was present.

In correspondence with the absence of branchial respiration during development, the branchial apparatus plays no great part in Reptiles, and often only the slightest traces of it are seen: thus in Snakes, for instance, only the hyoid remains, and this not always. In Chelonians a basal piece ("basihyobranchial") as well as the first branchial arch persist in addition (Fig. 76).
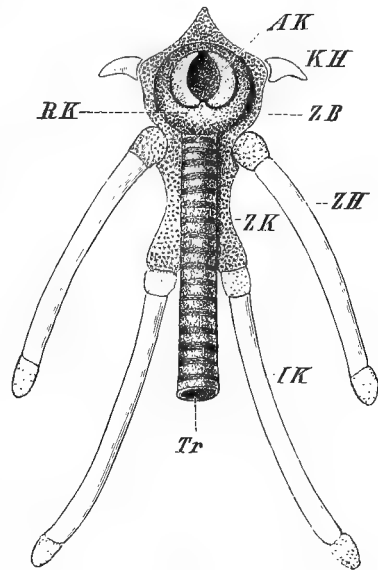


FIG. 76.—HYOBRANCHIAL APPARATUS WITH LARYNX AND TRACHEA OF *Emys europæa*.

*ZH*, basihyobranchial, which widens at *ZB* and bears the cricoid (*RK*) and arytenoid (*AK*) cartilages of the larynx; *KH*, lesser hyoid cornua; *ZH*, greater hyoid cornua; *IK*, first branchial arch; *Tr*, trachea.

E. **Birds.**

The skull of Birds is formed on a similar plan to that of Reptiles—more particularly of Lizards, but it exhibits certain special characteristics (Fig. 77).

The brain-case is proportionately very large, and all the cranial bones show a tendency to run together by the obliteration of the sutures originally present between them; they are usually delicate and spongy ("pneumatic"), thus contrasting greatly with those of Reptiles.[1]

Only in the region of the nose does the cartilage persist throughout life to any extent, and even here not always.

[1] It should, however, be mentioned that the development of air spaces within the bones of the skull is hinted at in Crocodiles and certain fossil Reptiles.

The *unpaired* occipital condyle no longer lies at the posterior boundary of the skull, but becomes relatively shifted forward along its base, so that the axis of the latter lies at an angle with that of the vertebral column.

The basis cranii is formed by a basioccipital and a basisphenoid, from which latter a bony rostrum, the remains of the anterior part of the parasphenoid, extends forwards. The posterior part of the parasphenoid persists as a large plate, the *basitemporal*, which underlies the basisphenoid and part of the basioccipital. Above the rostrum a small presphenoid is present in the embryo, and orbitosphenoids and alisphenoids are better developed than in Lizards. The auditory capsules ossify by three centres, and the relations of the tympanic cavity, auditory fenestræ, and columella are very similar to those of Reptiles. The two Eustachian tubes open together in the middle line.

The quadrate is movable upon the skull, as is also the whole maxillopalatine apparatus ; the palatopterygoid bar is separated from its fellow in the middle line and slides on the rostrum of the basisphenoid, thus allowing the beak to be raised or lowered to a greater or less extent : a complete bony palate comparable to that of Crocodiles is consequently never present. This mobility of the upper jaw is most marked in Parrots, in which the frontonasal joint forms a regular hinge.

The vomers, which may be absent, usually unite with one another, and with the palatines in a greater or less degree.[1] The posterior nostrils are always situated between the vomers and palatines. The maxilla and quadrate are connected by a jugal and a quadratojugal, and a squamosal is present ; small bones may also occur in the neighbourhood of the lachrymal. (For other details, compare Fig. 77.)

Teeth were present in Jurassic and Cretaceous Birds (Archæopteryx, Hesperornis, Ichthyornis), but are no longer developed in existing forms, their place being taken functionally by horny sheaths covering the bones of the jaws, which thus form a beak, much as in Chelonians.

Several bones are developed in connection with the lower jaw, the relations of which are essentially similar to those seen in Reptiles : they, however, become fused together in the adult, and the two rami of the mandible unite distally by synostosis.

The visceral skeleton is greatly reduced, though the basihyal and basibranchial—which are embedded in the tongue, as well as the first branchial arch persist, and the latter may, as in the Woodpecker, grow out into a pair of very long jointed rods extending far over the skull.

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[1] The differences in details as regards the arrangement of the bones of the palate are important for purposes of classification.
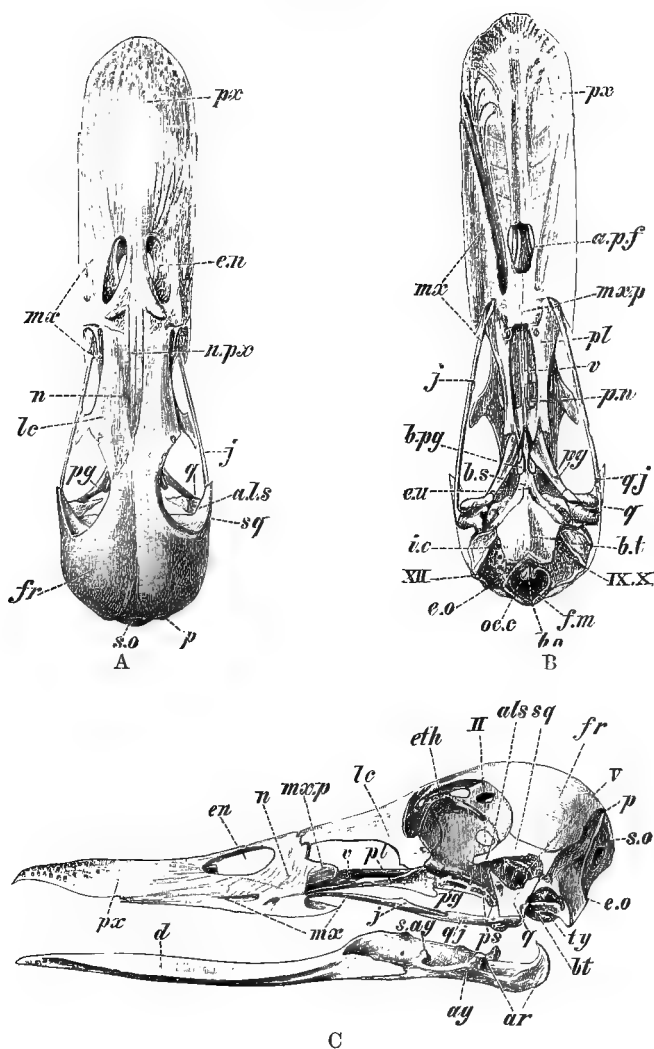
FIG. 77.—SKULL OF A WILD DUCK (*Anas boschas*). A, from above; B, from below; C, from the side. (From a preparation by W. K. Parker).

*a.l.s*, alisphenoid; *ag*, angular; *ar*, articular; *a.p.f*, anterior palatine foramen; *b.t*, basitemporal; *b.o*, basioccipital; *b.pg*, basipterygoid; *b.s*, basisphenoid; *d*, dentary; *e.n*, external nostrils; *eth*, ethmoid; *e.o*, exoccipital; *e.u*, Eustachian aperture; *fr*, frontal; *f.m*, foramen magnum; *i.c*, foramen for internal carotid artery; *j*, jugal; *lc*, lachrymal; *mx.p*, maxillopalatine process; *mx*, maxilla; *n*, nasal; *n.px*, nasal process of the premaxilla; *px*, premaxilla; *p*, parietal; *ps*, presphenoid; *pg*, pterygoid; *pl*, palatine; *p.n*, internal nostrils; *q*, quadrate; *q.j*, quadratojugal; *sq*, squamosal; *s.o*, supraoccipital; *ty*, tympanic cavity; *v*, vomer; *II*, foramen for optic nerve; *V*, for trigeminal; *IX*, *X*, for glossopharyngeal and vagus; *XII*, for hypoglossal.

### F. **Mammals.**

In Mammals there is a much closer connection between the
cranial and visceral regions of the skull than is the case in the
Vertebrates already described. In the fully-developed skull
both maxillary and palatopterygoid regions are united to
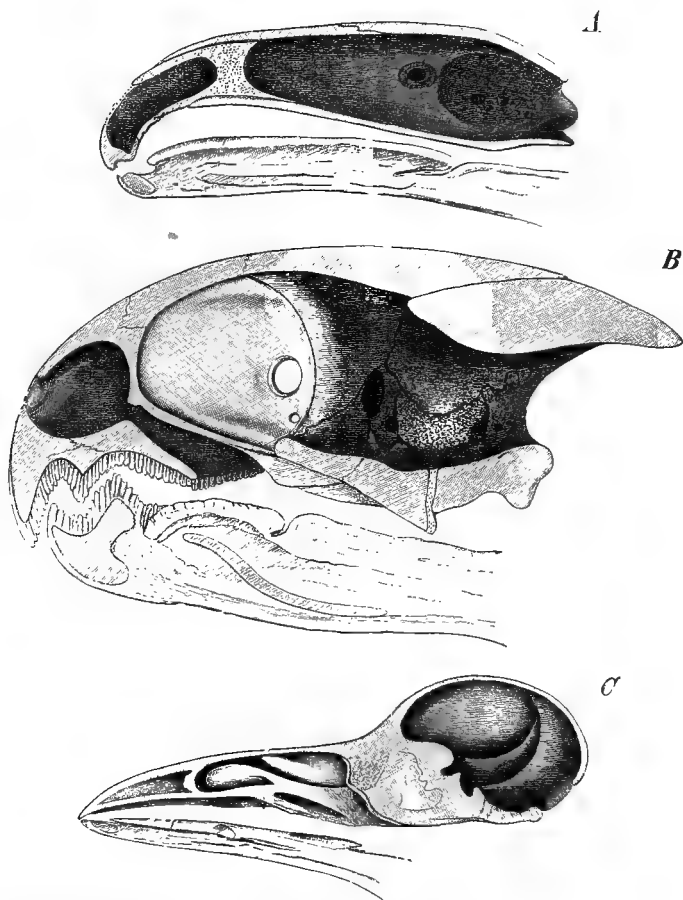


FIG. 78 A.—LONGITUDINAL VERTICAL SECTIONS THROUGH THE SKULLS OF—A,
*Salamandra maculosa*, B, *Testudo græca*, AND C, *Corvus corone*, TO SHOW THE
RELATIONS BETWEEN THE CRANIAL AND VISCERAL PORTIONS.

the cranium, though a facial and a cranial region can still be
distinguished. The higher we pass in the Mammalian series,
the more does the former come to lie below instead of in front of
the latter. In Man the facial skeleton is proportionately small

when contrasted with the large cranial portion of the skull, and the reduction of the angle between the basi-cranial and
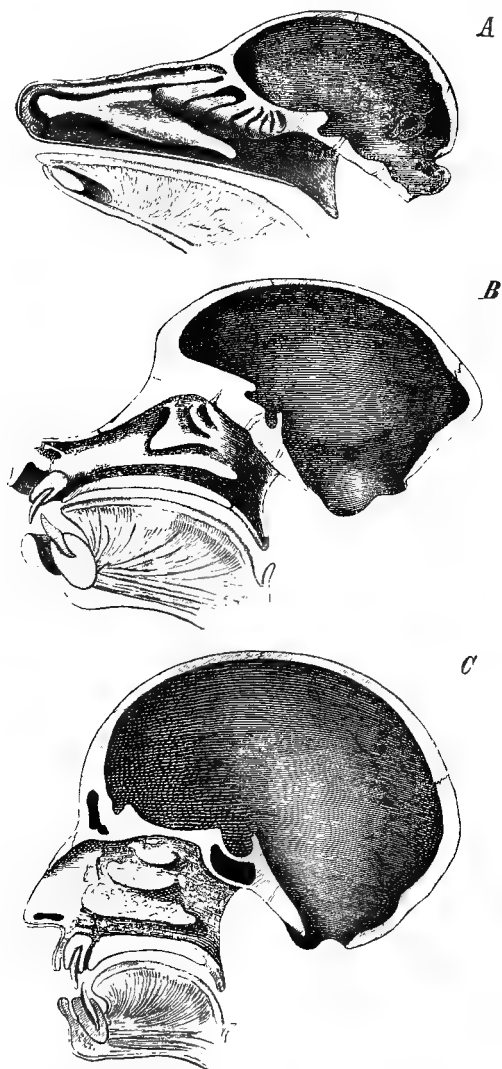


Fig. 78 ɪ.—Longitudinal Vertical Sections through the Skulls of A, Deer, B, Baboon, and C, Man, to show the Relations between the Cranial and Visceral Portions.

vertebral axes is carried still further than in Birds (comp. Figs. 78 A and B).

The base of the skull is mainly preformed in cartilage, as in Reptiles and Birds. The parasphenoid has practically disappeared,

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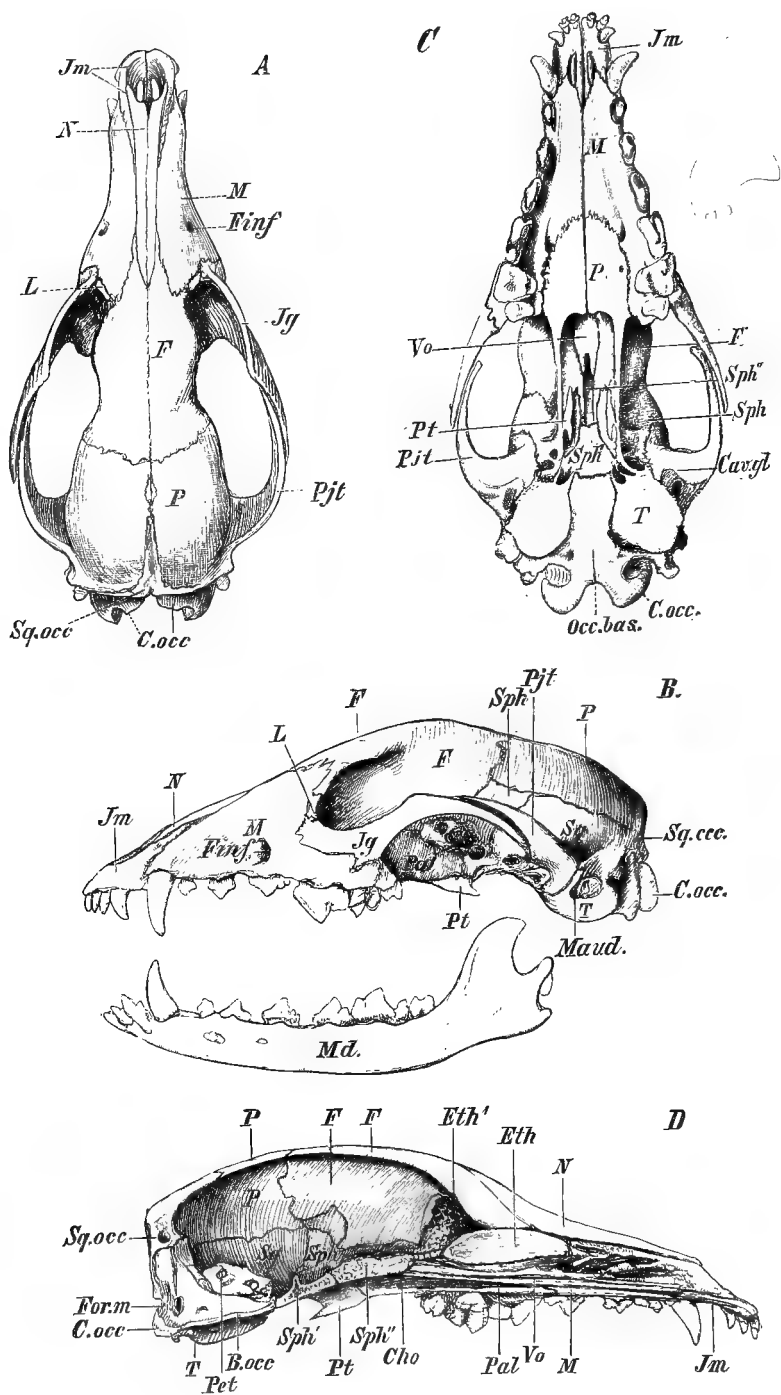
Fig. 79.—Skull of Greyhound. A, from above ; B, from the side ; C, from below ; and D, in longitudinal section.

*Jm*, premaxilla ; *N*, nasal ; *M*, maxilla, with the infraorbital foramen (*Finf*) ; *Jg*, jugal ; *Sq*, squamosal ; *Pjt*, zygomatic process of the squamosal ; *L*, lachrymal, surrounding the lachrymal canal ; *P*, parietal ; *Sq.occ*, supraoccipital ; *C.occ*, occipital condyles, on the exoccipitals ; *B.occ*, *Occ.bas*, basioccipital ; *Pal* (*P* in *C*), palatine ; *Pt*, pterygoid ; *Sph*, alisphenoid ; *Sph'*, basisphenoid ; *Sph''*, presphenoid ; *Maud*, external auditory meatus ; *T*, tympanic ; *For.m*, foramen magnum ; *Pet*, petrous portion of periotic ; *Cho*, posterior narial passage ; *Vo*, vomer ; *Eth*, lamina perpendicularis of the ethmoid ; *Eth'*, cribriform plate ; *Car.gl*, glenoid cavity for the lower jaw.

the anterior part of the basis cranii being formed by the ossification of the cartilage : this either gives rise to a distinct presphenoid (Marsupials, Rodents, and some Insectivores), or may be due to a union of the basal parts of the two orbitosphenoids. Alisphenoids, as well as a basisphenoid, a basioccipital, a supraoccipital, and exoccipitals are always present, the *paired* condyles being furnished by the exoccipitals (Fig. 79). The cranial cavity is closed in anteriorly by the bony lamina cribrosa or cribriform plate of the ethmoid, which has numerous perforations for the olfactory nerves in all Mammals but Ornithorhynchus.

The auditory capsules are ossified from prootic, epiotic, and opisthotic centres, which early fuse together to form the *periotic* or *petromastoid* bone. The denser internal (petrous) portion of this encloses the essential part of the organ of hearing, and a fenestra ovalis and fenestra rotunda are present on its outer surface : the more spongy mastoid portion reaches the surface of the skull between the exoccipital and the *tympanic* bone.[1] The latter overlies the petrous portion of the periotic, and gives attachment to the tympanic membrane : in the Placentalia it forms the tubular external auditory passage or meatus, below which it usually expands into a *bulla tympani*, which encloses the tympanic cavity and communicates with the pharynx by means of the Eustachian tube. The "temporal bone" of human anatomy represents the fused periotic, tympanic, and squamosal.

The cranial cavity is roofed in by frontals, parietals, an interparietal, and a supraoccipital : these, like many of the other cranial bones, are united by sutures which usually persist, at any rate for a long time. Many of the bones are more or less spongy internally, and may contain definite air-sinuses.

Most of the true Ruminants are provided with *horns* projecting from the frontal bones ; these are of three kinds :—

In the *Cavicornia* (Bovinæ, Antelopinæ, Caprinæ, Ovinæ) hollow bony processes are developed from the frontals, which become enveloped by horn formed from the epidermis. In the *Cervidæ*, a solid membrane bone becomes developed in the dermis round each process of the frontal, with which it fuses. This grows out to form the antler, and after attaining its full development, the skin covering it dries up owing to the development of the "burr" at its base ;

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[1] According to Gaupp, the tympanic corresponds to the "paraquadrate" of Amphibia and Reptilia (pp. 85 and 92).

this constricts the vessels, and the antler, being deprived of nutriment, falls off periodically at the close of the breeding season. In the young animal, the antlers are simple, but year by year they become more complicated and branched. *Giraffes* possess persistent antlers covered by hair and without any process from the frontal : they do not become anchylosed to the latter bone. The differentiation into horned and antlered forms first began in the Miocene epoch.

In the nasal cavity, scroll-like *turbinals* [1] are present : these are preformed in cartilage, and unite with the surrounding bones. The two nasal chambers are separated from one another by a cartilaginous septum nasi, the posterior part of which becomes ossified by a vertical plate (mesethmoid) in connection with the lamina cribrosa. The vomer, which is unpaired in the adult, is situated immediately below the nasal septum. Cartilage is retained only in the latter region and around the external nostrils ("aliseptal" and "alinasal cartilages"). The nasal cavities communicate anteriorly with the mouth by means of the incisive or naso-palatine canals as well as posteriorly by the internal nostrils.

As regards the structure of the hard palate, Mammals agree essentially with Crocodiles, but the small pterygoids (except, *c.g.*, in Anteaters and some Cetaceans) do not take part in its formation. The palate is very long in Echidna and in certain Edentata and Cetacea, and often (*e.g.*, Marsupialia) presents unossified vacuities.

The premaxilla takes an important part in enclosing the nasal cavity : it also contributes to the hard palate, and surrounds the nasopalatine canal. In the lateral parts of the face of most Mammals, the jugal or malar connects the maxilla with a process of the squamosal (instead of with the quadrate, as in Amphibia and Sauropsida) : thus a *zygomatic arch* is formed from these three bones (Fig. 79). In most cases (*e.g.*, Ungulata and Primates) the jugal is also connected with a process of the frontal, and thus the orbit becomes more or less completely separated from the temporal fossa.

The tympanic membrane is connected with the membrane of the fenestra ovalis by an articulated chain of small *auditory ossicles*, extending across the tympanic cavity and consisting of the *malleus, incus* (with its orbicular apophysis), and *stapes*—instead of by a single columella as in Amphibians and Reptiles. The two former of these bones arise in the embryo from the proximal end of the mandibular arch, one portion of which becomes constricted off to form the incus and another the malleus, both portions afterwards becoming ossified. The part of the arch in the lower jaw, distal to the malleus, corresponds to Meckel's cartilage, and in Fig. 80 the two are seen still in continuity. The stapes, which is stirrup-shaped in all Mammals but Monotremes and certain Marsupials and Edentates, plugs the fenestra

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[1] For details of the turbinals in Mammals and other Vertebrates, compare the section on the olfactory organ.

ovalis on the one hand and articulates with the incus on the other, while the malleus articulates with the incus, and its manubrial process is attached to the tympanic membrane. The above facts indicate that the malleus corresponds to the *articular* element of the mandible of lower Vertebrates, and the incus to the *quadrate*.

The morphology of the stapes is not by any means clear ; phylogenetically it certainly corresponds to the upper end of the hyoid arch (pharyngo-hyal or hyomandibular of Fishes), but its homology with this element has not been proved ontogenetically. Its basal plate, however, doubtless corresponds to the stapedial plate of Amphibia and Sauropsida (comp. pp. 84 and 92).
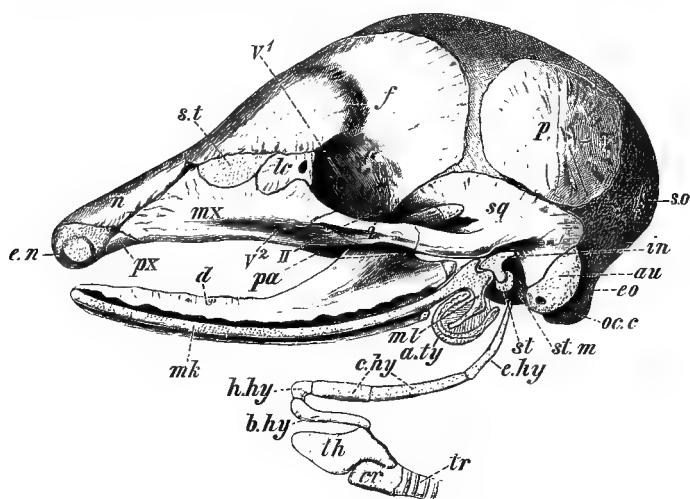


FIG. 80.—SKULL OF EMBRYO OF ARMADILLO (*Tatusia hybrida*).    (Modified from a drawing by W. K. Parker.)

*a.ty*, tympanic annulus ; *au*, auditory capsule ; *b.hy*, basihyal ; *c.hy*, ceratohyal ; *cr*, cricoid ; *d*, dentary ; *e.hy*, epihyal ; *e.n*, external nostril ; *eo*, exoccipital ; *f*, frontal ; *h.hy*, hypohyal ; *i*, jugal ; *in*, incus ; *lc*, lachrymal ; *mk*, Meckel's cartilage ; *ml*, malleus ; *mx*, maxilla ; *n*, nasal ; *oc.c*, occipital condyle ; *p*, parietal ; *pa*, palatine ; *px*, premaxilla ; *so*, supraoccipital ; *st*, stapes ; *s.t.* superior turbinal ; *st.m*, stapedius muscle ; *sq*, squamosal ; *th*, thyroid ; *tr*, trachea ; $V^1$, $V^2$, foramina through which the first and second divisions of the trigeminal pass out from the orbit ; *II*, optic foramen.

Thus the parts of the mandibular arch which form the hinge of the jaw in lower Vertebrates are in Mammals utilised to conduct sound-vibrations to the internal ear. Around Meckel's cartilage a membrane-bone is developed corresponding essentially to the dentary ; this forms the entire lower jaw of the adult and develops a new articulation with the *squamosal* : this arrangement is characteristic of and confined to the Mammalia (Figs. 79 and 80). The two rami of the mandible usually unite distally.

Teeth, which are only exceptionally wanting (*e.g.*, Echidna.

certain Edentates), are confined to the premaxilla, maxilla, and mandible.

The *hyoid arch* (Fig. 80) is connected proximally with the auditory capsule and distally with the base of the third visceral (that is, the first true branchial) arch. It becomes more or less ossified, but the greater part is usually reduced to a fibrous band, and may be quite rudimentary; its proximal end forms the styloid process of the periotic, and its distal the lesser (anterior) cornua of the so-called hyoid bone of the adult. The body of this bone represents the basal parts of the hyoid and first branchial arch, the greater (posterior) cornua belonging to the latter.

<div align="center">VI. LIMBS</div>

The problem of the origin and morphological meaning of the fins and limbs of Vertebrates is one which, in point of interest and importance, is comparable to that relating to the head. During the last thirty years it has been attacked vigorously both from the embryological and the palæontological sides, and has given rise to so many speculations—often of a very contradictory nature—that only the barest outline of some of the more important results obtained can be given in the course of the present chapter.

The fins or limbs, which are distinguished from the *axial organs* (head, neck, and body), as *appendicular organs*, serve mainly for locomotion, and may be divided into two groups, the *unpaired* and the *paired* (pectoral and pelvic).

<div align="center">A. <strong>Unpaired Fins.</strong></div>

The unpaired, or median fins, which are mainly characteristic of Fishes, arise in the embryo as a ridge of the integument (epiblast and mesoblast) extending along the median dorsal line from the anterior part of the trunk backwards to the tail, around the apex of which it is continued forwards for some distance along the ventral side : thus a dorsal, caudal, and ventral portion can be distinguished. In the course of further development, these portions either remain continuous, or else certain parts undergo reduction, so that the ridge only persists in certain regions, where it forms independent *dorsal, caudal,* and *ventral* or *anal fins* (Fig. 81, A, B): in these regions muscles and skeletal parts become developed.[1]

These skeletal parts consist of supporting rays of two kinds. In the base of the fin *cartilaginous radii*, usually segmented, are

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[1] The curious suctorial disc on the dorsal side of the head of the Teleostean Remora (Echeneis), by means of which it attaches itself to foreign objects, arises in the embryo from the anterior portion of the dorsal unpaired fin, and this is indicated throughout life by the arrangement of the blood-vessels, nerves, and skeletal parts.

formed in all the Fishes proper and in Dipnoans ; these, which
may conveniently be distinguished as *"pterygiophores,"* may unite
to form a *basipterygium*, and in bony Fishes they become ex-
tensively ossified : they frequently come into secondary con-
nection with the vertebral column (*e.g.,* by means of the so-called
" interspinous bones" of Teleostei).    The peripheral part of the
fin is supported by *dermal rays*, which may consist of numerous
delicate *horny* fibres (*e.g.,* Marsipobranchs, Elasmobranchs, Cartilag-
inous Ganoids, Dipnoans), or of *bony* rods, entire or jointed, often
cleft at the base, and *not* preformed in cartilage (Teleosts, Bony
Ganoids).

Median fins are also present in the Amphibia, in which they
may persist throughout life (*e.g.,* Perennibranchiata), or may only
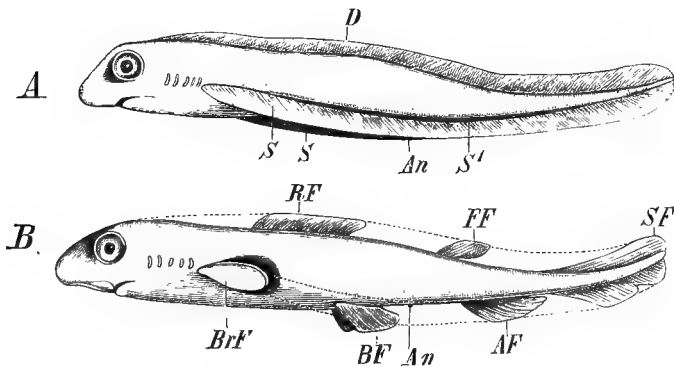


FIG. 81.—DIAGRAM SHOWING (A) THE UNDIFFERENTIATED CONDITION OF THE
PAIRED AND UNPAIRED FINS IN THE EMBRYO, AND (B) THE MANNER IN
WHICH THE PERMANENT FINS ARE FORMED FROM THE CONTINUOUS FOLDS.

*D,* dorsal fin-fold ; *S, S*, lateral folds, which unite together at *S¹* to form the
ventral fold ; *RF, FF*, dorsal fins ; *SF*, tail-fin ; *AF*, anal fin ; *BrF*, pectoral
fin ; *BF*, pelvic fin ; *An*, anus.

occur in the larval stage and occasionally also during the breeding
season (*e.g.* Newt).    They have the form of a continuous in-
tegumentary fold extending round the tail and along the back
for a greater or less distance, but enclose *no skeletal elements*.

Amongst Reptiles, median fins were present in Ichthyosaurus,
and these are comparable to the dorsal fins occurring in the
Cetacea amongst Mammals : in both cases they must be looked
upon as structures acquired secondarily in connection with an
aquatic existence.

B.    **Paired Fins or Limbs.**

Embryological researches have shown that *lateral fin-folds* must
have existed in the ancestors of Vertebrates in addition to the

median fins, and these can still be recognised in young embryos
of Elasmobranchs (Fig. 81, A) and to a less extent in those of
Sturgeons, Teleosts, and Amphibians.    They extended backwards
along the sides of the body from just behind the head, gradually
converging towards the anal region, where they became continuous
with the ventral part of the median fin-fold (Fig. 81, A), and thus
resemble the *lateral* or *metapleural folds* present in the adult
**Amphioxus.**    As is usually the case in the median fins (p. 102),
certain parts of these lateral folds have undergone reduction,
only the anterior and posterior portions remaining to form *two*
paired (pectoral and pelvic) fins or limbs, which must therefore be
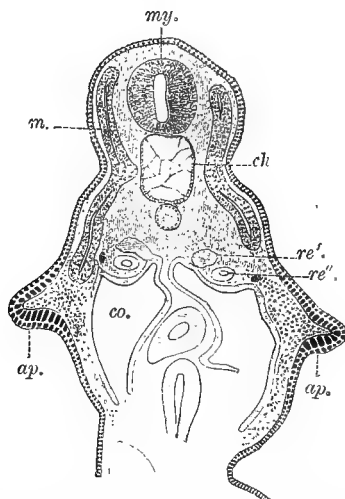


FIG. 81, A.—TRANSVERSE SECTION THROUGH THE EMBRYO OF A SHARK (*Pristiurus
melanostomus*), 9 MM. LONG, SHOWING THE MODE OF ORIGIN OF THE PEC-
TORAL LIMB-BUDS (*ap.*).

*ch*, notochord ; *co*, cœlome ; *m*, myomeres, seen to be growing ventrally ; *my*,
spinal cord.

looked upon as the localised remains of a continuous lateral fin-fold
on either side of the body, and as being homodynamous (*i.e.*, serially
homologous) structures.

Into these paired fins the myotomes extend, and cartilaginous
supports (pterygiophores) are formed from the mesoblast, as in the
case of the median fins.    These radii appear first of all at the base
of the fin, gradually extending centrifugally into the latter, and
also, becoming fused, centripetally into the body-wall.    An articula-
tion is then secondarily formed between the fused basal part of the
skeleton situated in the free portion of the limb (*basipterygium*) and
that which extends into the lateral body-wall and serves as a support
for the limb proper : this latter portion constitutes the *limb-arch*
or *girdle*.    The arch may remain comparatively small and not extend

far dorsally; but when the limb is destined to perform more important movements in locomotion, or to give a more definite support to the body, the arch may extend upwards so as to come into connection with the axial skeleton as well as meeting with its fellow ventrally, thus forming an almost complete girdle around the body. The limb skeleton may become ossified later.
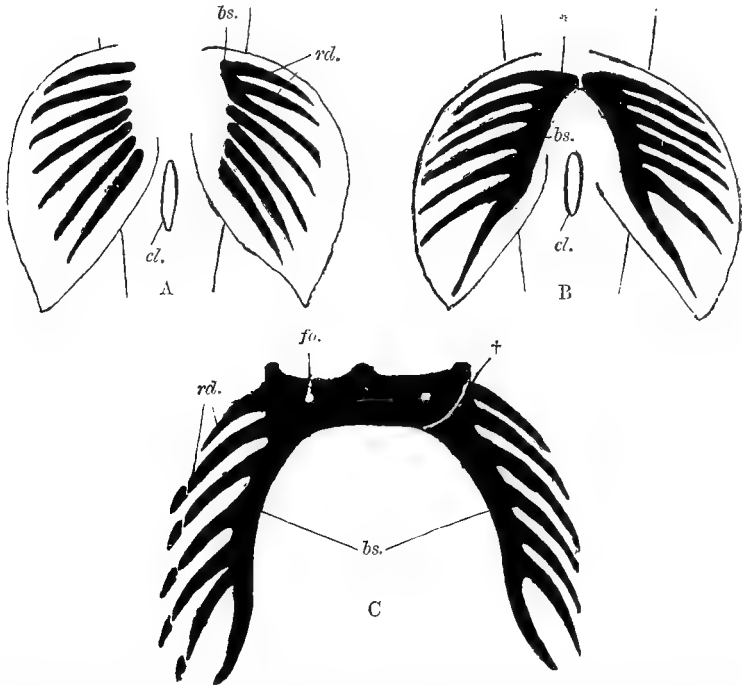


FIG. 82.—A, B, C. DIAGRAM OF THREE SUCCESSIVE STAGES IN THE DEVELOPMENT OF THE PELVIC FIN OF A SHARK.

*rd*, primitive radii, which in A are beginning to fuse into a basal plate (*bs*). In B this fusion has taken place on both sides, and at * the proximal ends of the two basals are approximating to form the arch. In C the process is completed, and at † an articulation has been formed between the arch and the free portion of the fin. On the left side in C the radii are becoming secondarily segmented. *fo*, obturator foramen; *cl*, cloacal aperture.

In the case of Fishes, the pelvic fin as a rule remains at a simpler and more embryonic stage than the pectoral.

The paired limbs are not connected with any particular body-segments, but vary greatly in their relative positions and in the number of nerves which supply them.

The essential part of this conception as to the origin of the paired limbs is due to Thacher, Mivart, Balfour, Haswell, and Dohrn.[1] Gegenbaur had

[1] A somewhat similar idea was put forward by Goodsir as early as 1856.

previously put forward the view that the arches and fins correspond to meta-morphosed gill-arches and rays : he supposed that one ray came to exceed the others in size, and that the others then gradually became attached to it instead of to the arch, the result being a *biserial* form of fin ("*archiptery-gium*") which is most nearly retained in Ceratodus (Fig. 101 and p. 124).

## Pectoral Arch.

**Fishes and Dipnoans.**—Paired fins and arches are wanting in the Cyclostomi. In the Elasmobranchii and Holocephali the pectoral arch consists of a comparatively simple cartilaginous bar
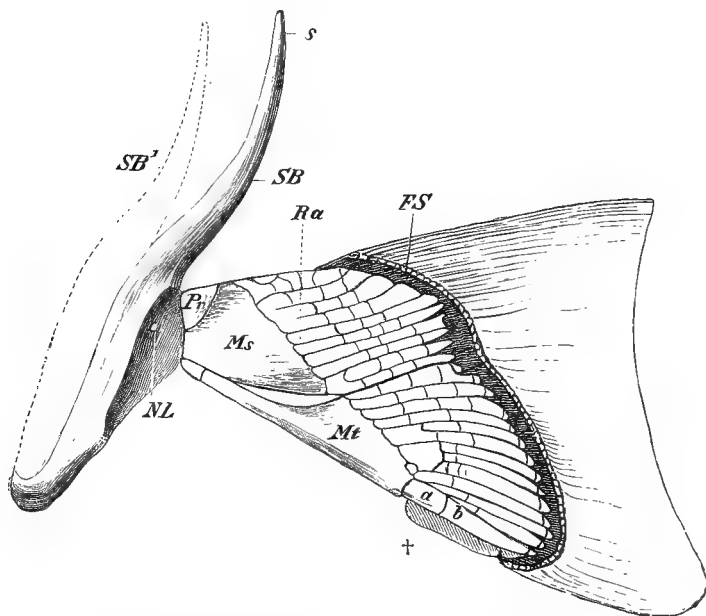
FIG. 83.—PECTORAL ARCH AND FIN OF *Heptanchus*.

*SB*, *SB*[1], pectoral arch, with a nerve aperture at *NL* ; *Pr*, *Ms*, *Mt*, the three basal elements of the fin—pro-, meso-, and metapterygium ; *Ra*, cartilaginous fin-rays ; *a*, *b*, the main fin-ray, lying in the axis of the metapterygium ; †, single ray on the other side of the axis (indication of a biserial type) ; *FS*, horny rays, cut through.

the two halves of which are united ventrally by cartilage or fibrous tissue (Fig. 83), and in embryos of Ganoids and Teleosts it has at first a similar structure.

Later, however, in both the last-named groups, a row of bony structures arises in the perichondrium in this region ; so that a *secondary* or bony pectoral arch may be distinguished from a *primary* or cartilaginous one, the latter becoming less marked in proportion to the development of the former (Fig. 84).

The free extremity, or fin, is always connected with the hinder

and outer circumference of the (primary) arch, *convex* articulations being formed on the arch which fit into *concave* facets on the fin, the point of attachment of which may be taken as separating the arch into an upper dorsal and a lower ventral section. The former, which may exceptionally be connected with the vertebral column (viz., Raiidæ), corresponds to a *scapula*, and the latter to a *coracoid* plus *procoracoid* of the higher Vertebrata.[1]

In Teleosts and Bony Ganoids the bony (secondary) arch forms the principal support of the fin in the adult, the main element being a large *clavicle*. The primitive relations are thus much altered. The arch becomes secondarily connected with the skull. (For further details, compare Fig. 84.)

**Amphibia.** — In this Class the pectoral arch shows no direct connection with that of Fishes, but is similar in plan to that of all the higher Vertebrates.



FIG. 84.—LEFT PECTORAL ARCH AND FIN OF THE TROUT. (From the outer side.)

*D*, *D*[1], *D*[2], chain of secondary bones of the pectoral arch (clavicle and supra-clavicle), which is connected with the skull by means of the post-temporal (*Cm*) ; *S* and *Co(Cl)*, bony scapula and coracoid, which have become developed in the cartilage (*Kn*) ; *L* foramen in scapula ; *M*[1], metapterygium ; *Ra*, *Ra*, the second and third, and 4, the fourth basal element of the fin ; *Ra*[1], the second cartilaginous row of radii ; *HS*, bony ray on the border of the fin which is connected with the fourth basal element ; *F*,*S*, bony fin-rays, shown cut away from their attachments.



FIG. 85A.—DIAGRAM OF THE GROUND TYPE OF PECTORAL ARCH MET WITH IN ALL VERTEBRATA FROM AMPHIBIA UP TO MAMMALIA.

*S*, scapula ; *Co*, coracoid ; *Cl*, procoracoid ; *H*, humerus.

It always consists on either side of a cartilaginous or bony dorsal plate (*scapula*), which curves round the side of the body and becomes continuous ventrally with two processes—an anterior (*procoracoid*) and a posterior (*coracoid*) (Figs. 85A and B). The ventral part of the arch becomes connected with the sternal apparatus (compare Fig. 43). The humerus articulates with a *concave* glenoid facet at the junction of the scapula and coracoid. The two coracoid plates either overlap one another in the mid-ventral line (Uro-

[1] The pectoral arch of Dipnoans is intermediate in character between that of Elasmobranchs and Ganoids. It shows so many special peculiarities as regards form and position that it cannot be fully described here.

deles and certain Anura—*e.g.*, Bombinator, Fig. 43, C), or else their free edges come into apposition and fuse together (other Anura, *e.g.*, Rana, *see* Fig. 43, D). In Anurans the procoracoids have a more transverse position than in Urodeles, and come into
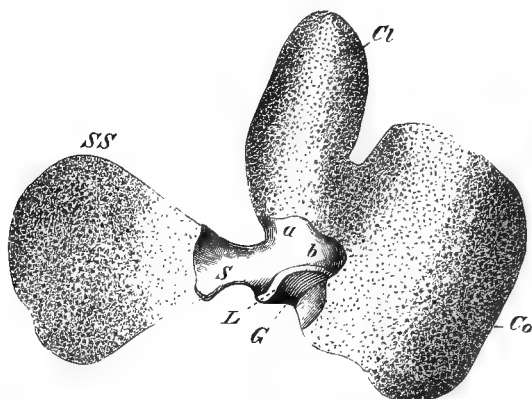


FIG. 85B.—PECTORAL ARCH OF THE RIGHT SIDE OF *Salamandra maculosa*, considerably magnified, and flattened out.

*SS*, supra-scapula ; *S*, scapula (ossified) ; *Co*, coracoid ; *Cl*, procoracoid ; *a, b,* bony processes extending into the procoracoid and coracoid respectively ; *G*, glenoid cavity, surrounded by a rim of cartilage (*L*).

connection with the coracoid in the mid-ventral line, thus giving rise to a fenestra between the two. The whole arch is, moreover, more strongly ossified, the procoracoid being covered by an investing bone—the *clavicle*.

**Reptilia.**—In Reptiles the ossification is still more marked. The simplest condition of the shoulder-girdle is seen in Chelonians



FIG. 86.—PECTORAL ARCH OF A CHELONIAN. (Ventral view.)

*S*, scapula ; *Co*, coracoid ; *Co¹*, epi-coracoid ; *Cl*, procoracoid ; *B*, fibrous band between these two elements ; *Fe*, fenestra between them ; *G*, glenoid cavity.

(Fig. 86), in which its similarity to that of Amphibians as well as to that of Hatteria is at once seen : no clavicle is developed.

In other Reptiles the same general plan is retained with modifications. Thus in Lizards (Fig. 44) the well-developed clavicle is more independent of the rest of the arch and becomes ossified directly, forming a delicate secondary bony lamella extending from the scapula to the apex of the episternal apparatus. But it must be remembered that the undifferentiated cells of which it at first consists are in direct continuity with those which form the scapula. Unossified spaces are left in the coracoid, giving

rise to fenestræ closed over by fibrous membrane. In Crocodiles and Chameleons the clavicles are either wanting or rudimentary.

The presence of a pectoral arch in numerous footless Reptiles (certain Skinks, Amphisbænians) indicates that they formerly possessed extremities ; rudiments of the latter may even be seen in the embryo though they disappear entirely later on (*Anguis fragilis*). (For the peculiar pectoral arch of the Stegocephala, *see* Fig. 46.)

**Birds.**—In Birds, the scapula consists of a thin and narrow plate of bone often extending far backwards, the strong coracoid being bent at a sharp angle with it in all Carinate Birds (Fig. 41). The lower end of the latter is firmly articulated in a groove on the anterior edge of the sternum.

In almost all Flying Birds the clavicle is well developed, and becomes united with its fellow to form a *furcula* (comp. p. 63 and Fig. 41). It is formed as a membrane bone investing a band of cartilage present in the embryo in this region.

Amongst the Cursorial Birds, the Emeu and Cassowary possess rudimentary clavicles : in the others they are wanting. They have also undergone reduction in some Carinate Birds (*e.g.*, certain Parrots).

**Mammals.**—In Monotremes only amongst Mammals does the coracoid extend ventrally to reach the sternum (Fig. 48) ; in all other members of this Class it characteristically becomes reduced, and simply forms a prominent process on the scapula (*coracoid process*), which becomes ossified from a separate centre.[1]

Thus the *scapula* alone serves to support the extremity; it becomes at the same time greatly broadened out, and gives rise on its outer side—in connection with the highly differentiated muscles of the limb—to a strong ridge (spina scapulæ), which extends downwards to form the so-called acromion. The distal end of the clavicle usually becomes connected with the acromion, its proximal end articulating with the anterior edge of the sternum.

In those Mammals in which the fore-limbs are capable of very varied and free movements, the clavicles are strongly developed. In others, such as the Carnivora and Ungulata, they may be entirely wanting or only rudimentary, and in the latter case their relations to the scapula become altered.

### Pelvic Arch.

**Fishes.**—The first rudimentary indications of a pelvis are seen in Cartilaginous Ganoids, amongst which, however, they present considerable variations—even in individuals of the same species. They consist of two calcified or even ossified *pelvic plates*, which

[1] According to Howes the coracoid process represents an epicoracoid (comp. Fig. 48), the coracoid itself being only occasionally indicated by a small centre of ossification on the glenoid margin of the scapula.

become segmented off from the basal cartilage (*basi-* or *metaptery-gium*) of the free fin. In some cases even this segmentation does not take place, and thus the pelvis remains undifferentiated. This simple condition is also met with in the ancient forms Pleura-canthus and Xenacanthus, and is essentially retained in Lepi-dosteus, Amia, and the Teleostei (Fig. 87).

In Polypterus, which most nearly resembles the Devonian Crossopterygii, the pelvis shows some advance on that of Sturgeons. Owing, doubtless, to the necessity of a firmer connec-tion of the fin with the body-wall, the two pelvic plates become
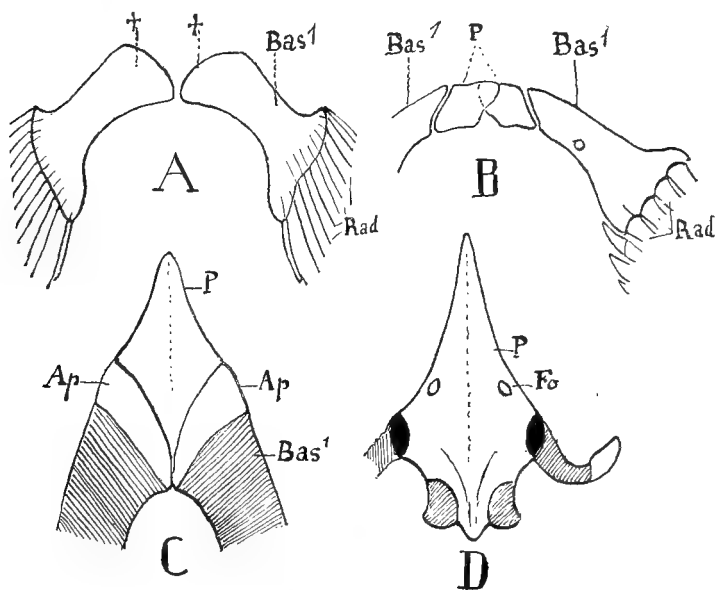


FIG. 87.—DIAGRAMS ILLUSTRATING THE PHYLOGENY OF THE PELVIS.

A, *Pleuracanthus*—the pelvis is here undifferentiated ††; B, *Scaphirhynchus cataphractus;* C, *Polypterus bichir;* D, *Necturus (Menobranchus)*. *Bas¹*, basipterygium ; *Ap*, its cartilaginous apophysis ; *P*, pelvis ; *Rad*, radii : *Fo*, obturator foramen.

united together in the mid-ventral line (Fig. 87, C) : but even here the basipterygium may remain in continuity with the pelvic plate on one or both sides. In spite, however, of the rudimentary character of the pelvis of Polypterus, the essential form of that of the Dipnoi and Amphibia is already sketched out.

The pelvis of the Elasmobranchii and Holocephali indicates that they early branched off from the ancestral stock. Instead of a small and narrow pelvic plate more or less elongated antero-posteriorly, the pelvis forms a transverse bar of considerable extent, developed in connection with the basipterygium (Fig. 82);

it is perforated by nerves, and gives rise on either side to an iliac process (most marked in Holocephali) extending into the lateral walls of the body (Fig. 88).

In all the above cases we may look upon the pelvic plate as essentially corresponding, more or less completely, with the *ischio-pubis* of higher forms.

**Dipnoi.** — The small cartilaginous pelvic plate (Fig. 89) is provided with a long and delicate anterior median, a short posterior median, and two pairs of lateral processes. Of the latter the anterior (prepubic processes) vary much in form and length, being much longer in Protopterus than in Ceratodus, and each is embedded



FIG. 88.—DIAGRAM OF THE ELASMOBRANCH PELVIS.
(From the ventral side.)

*BP*, Pelvic plate (ischio-pubis) ; *I*, iliac process ; *PP*, prepubic process ; *Cep*, epipubic process ; *Sy*, region of the ischiopubic symphysis ; *Fo*[1], obturator foramen ; *Bas*, *Pro*, *Rad*, basipterygium, propterygium, and radii of the fin.

in an intermuscular septum ; with the posterior the skeleton of the free fin is articulated by means of an intermediate piece. The anterior unpaired process must be looked upon as an epipubic process, corresponding with that of Amphibians, Reptiles, and Mammals (pp. 113, 115, 121).

**Amphibia.** —*Urodela.* — It will be seen by a glance at Fig. 87, D, that the ventral portion of the pelvic arch of Necturus is formed on the same plan as the pelvic plate of the Dipnoi and Crossopterygii, but, as in all Urodela and Amniota, it is perforated by the obturator nerve : this indicates a further lateral extension. Like the pelvis of all Vertebrates, it has a paired origin, and in Proteus and Amphiuma this is indicated by the fact that its



FIG. 89. —PELVIS OF *Protopterus*. (From the ventral side.)

*a*, prepubic process, which may become forked at its distal end ; *b*, process to which the hinder extremity (*HE*) is attached ; *Gr*, sharp ridge, for attachment of muscles ; *c*, epipubic process ; *M*, *M*, myotomes ; *M*[1], *M*[1], intermuscular septa.
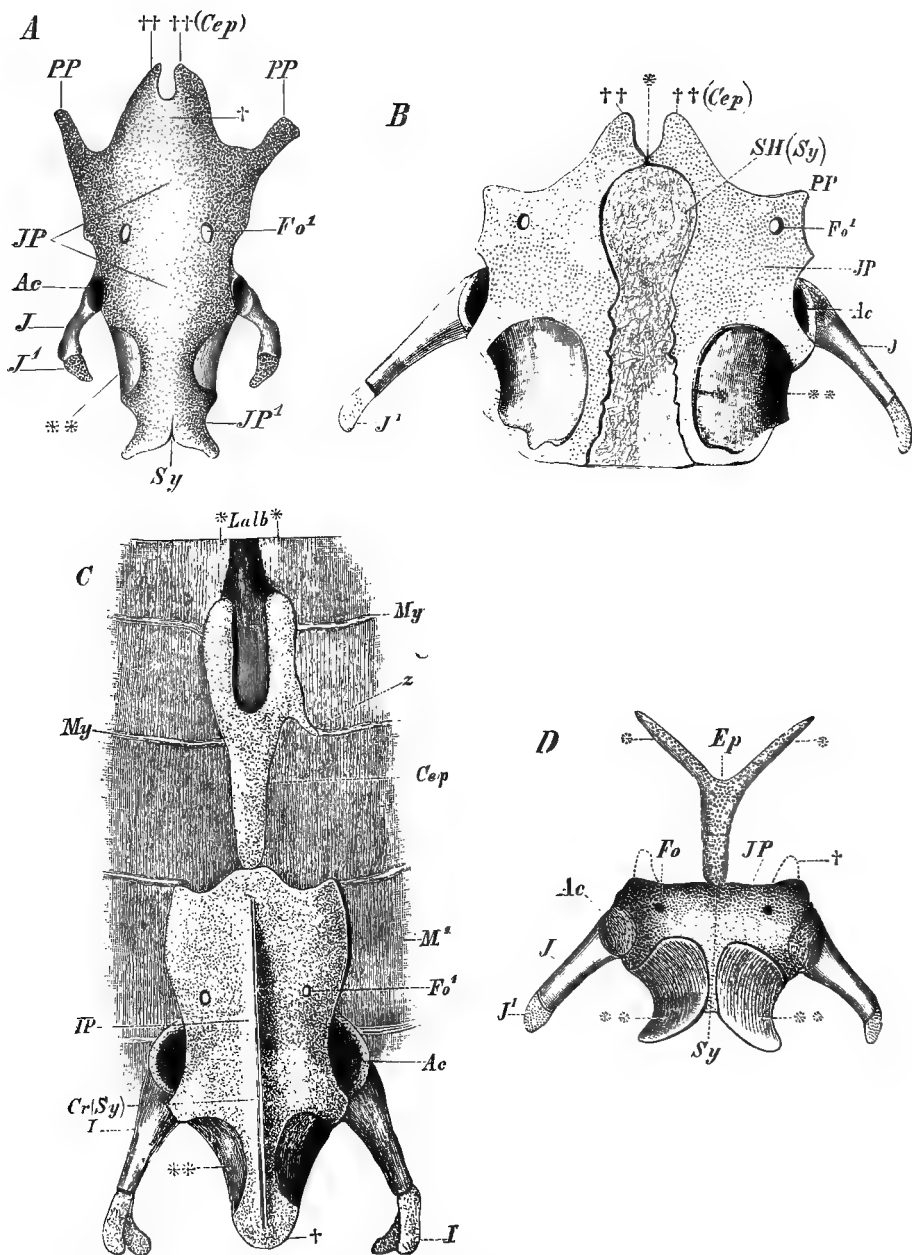
FIG. 90.—PELVIS OF (A) *Proteus*; (B) *Amphiuma*; (C) *Cryptobranchus*; AND (D) *Salamandra maculosa*. (From the ventral side.)

*JP, JP¹, IP*, ventral pelvic plate (ischio-pubis); ** (in *A*), ossified region of the ischium ; *PP*, prepubis ; †† (*Cep*), *Ep*, epipubis ; ** (in C and D) secondary bifurcation of the epipubis ; *z*, outgrowth from this bifurcation ; † (in C), hypoischiatic process, present in the Derotremata and Necturus ; *Sy*, symphysis, in which region a strong tendinous area (*SH*) exists in Amphiuma, the pubic regions only coming together in the middle line at * ; *Fo, Fo¹*, obturator foramen ; *Ac*, acetabulum ; *J, J¹, I, I¹*, ilium ; *Lalb*, linea alba ; *My*, intermuscular septa ; *Cr, (Sy)*, muscular ridge on the ventral side of the ischio-pubis.
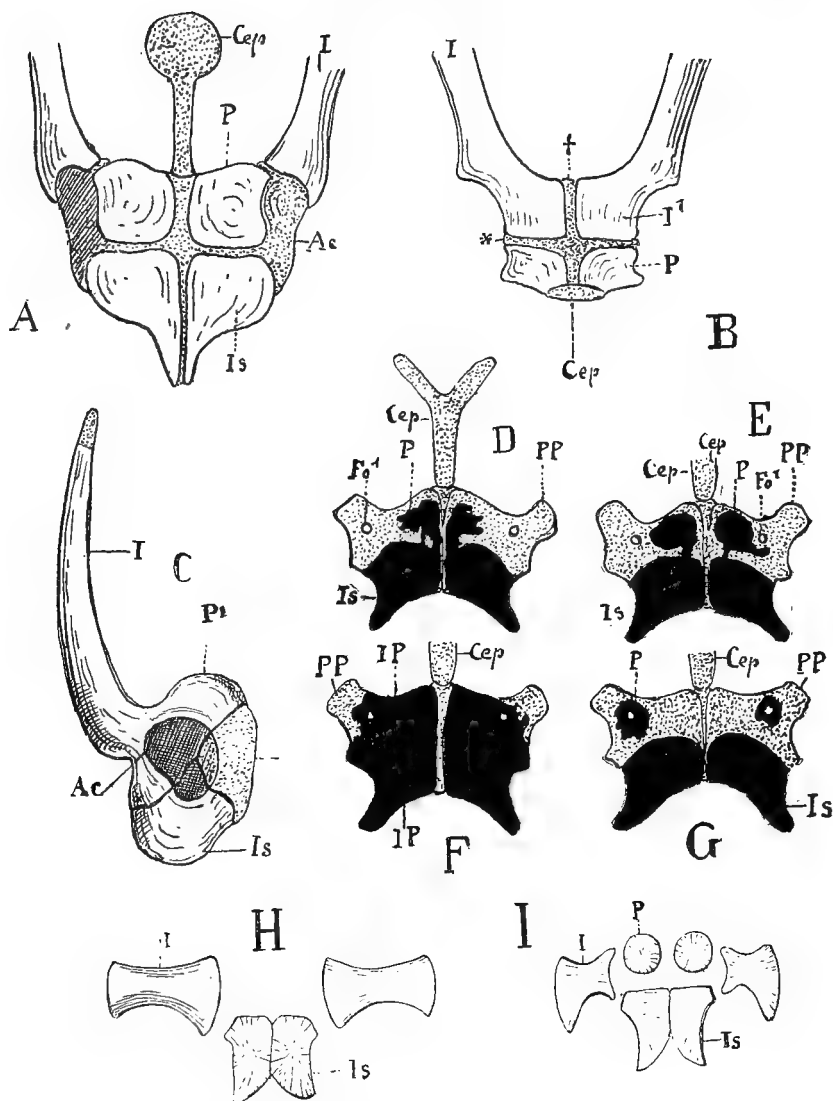
FIG. 91.—PELVIS OF VARIOUS AMPHIBIA. A, *Xenopus* (*Dactylethra*), from below ; B, the same from the front ; C, *Rana esculenta*, from the right side ; D and E, *Salamandra atra* ; F and G, *Salamandra maculosa* ; H, *Branchiosaurus* ; I, *Discosaurus*. D-I, from the ventral side. (Figs. H and I after Credner.)

*I*, ilium ; *Is*, ischium ; *P*, pubis (*P*<sup>1</sup> in *Rana*, pubic end of ilium) ; *IP*, fused ischio-pubic ossification ; *PP*, prepubis ; *Cep*, epipubic cartilage ; *Fo*<sup>1</sup>, obturator foramen ; *I*<sup>1</sup> (in Xenopus), the proximal end of the ilium, which is separated from its fellow and from the pubis by a +-shaped zone of cartilage, †, * ; *Ac*, acetabulum.

anterior epipubic process is paired throughout life (Fig. 90, A, B). In the Derotremata and Myctodera, on the other hand, the epipubis is unpaired from the first, owing probably to an abbreviation of development, its anterior end becoming bifurcated secondarily (Fig. 90, C, D).

As in Fishes and Dipnoans, the two halves of the ischio-pubic region tend to fuse together in the middle line to form an unpaired pelvic plate, but all kinds of modifications occur in this respect in adaptation to the movements of the hind-limb in different forms ; and, as in all cases the median zone of the plate represents the line of least resistance, the lateral halves may eventually become more or less distinct from one another.   The effect of the action of the muscles becomes, however, greater when the pubic region is more distinctly marked off from the ischium, and ossification takes place in it (*e.g.*, Salamandra atra and, more rarely, S. maculata).   Thus the typical triradiate arrangement of the pelvis (*ilium, ischium*, and *pubis*), such as is further differentiated in certain Stegocephala (Discosaurus) and in Reptiles, as well as in Xenopus, is already sketched out (Fig. 91).

An important difference between the pelvis of Ganoids and Dipnoans and that of Amphibians is seen in the marked development of the *iliac region* in the latter group.   The ilium, like the scapula, extends upwards in the lateral walls of the body (compare the iliac process of Elasmobranchs, Fig. 88), and in Proteus and Amphiuma, owing to the reduction of the limbs in these forms, does not reach the vertebral column (Fig. 90, A, B).   In all other Amphibia, as in the Amniota, it comes into connection with the sacrum (p. 45), owing to the necessity for the hind-limb to act as a support for the body in terrestrial animals, and not merely as an organ of propulsion, as in Fishes.



Fig.  92. — Pelvic Arch of Frog (*Rana esculenta*). From below.

*J, J¹*, ilium ; *Is*, ischium ; *P*, cartilaginous pubic region ; *Cr*, the median ventral ischio-pubic crest ; *G*, acetabulum ; *Oc*, urostyle ; *Pt*, transverse process of sacral vertebra.

*Anura.*—The pelvis of the Anura differs from that of Urodela in the following characteristics.   In correspondence with their mode of progression, the ilium of each side becomes extended so as to form a long rod (Figs. 91 *C*, 92) ; and the flat pelvic plate, which in Urodeles lies in the plane of the abdominal walls, becomes closely pressed together in the middle line and gives rise to a well-marked ventral keel : it is not perforated by the obturator nerve.   The pubic region, moreover, though often calcified, is independently ossified only in the case of Xenopus (Fig. 91, A,B).

**Reptiles.**—The chief characteristics of the Reptilian pelvis as

FIG. 93.—PELVIC ARCH OF VARIOUS REPTILES. (From the ventral side). A, *Palæohatteria*, after Credner ; A[1]-C, *Plesiosaurus* : A[1], from a restoration in the College of Surgeons ; B, from Huxley's *Anatomy of Vertebrated Animals;* C, after D'Arcy Thompson ; D, *Labyrinthodon rütimeyeri ;* E, *Hatteria.*

*P*, pubis ; *PP*, prepubis ; *Cep*, epipubic cartilage ; *Fo*[1], obturator foramen ; *Is*, ischium ; *I*, ilium ; †,†, ischio-pubic foramina ; *, hypoischiatic process, which becomes segmented off from the pelvis in other Reptiles.
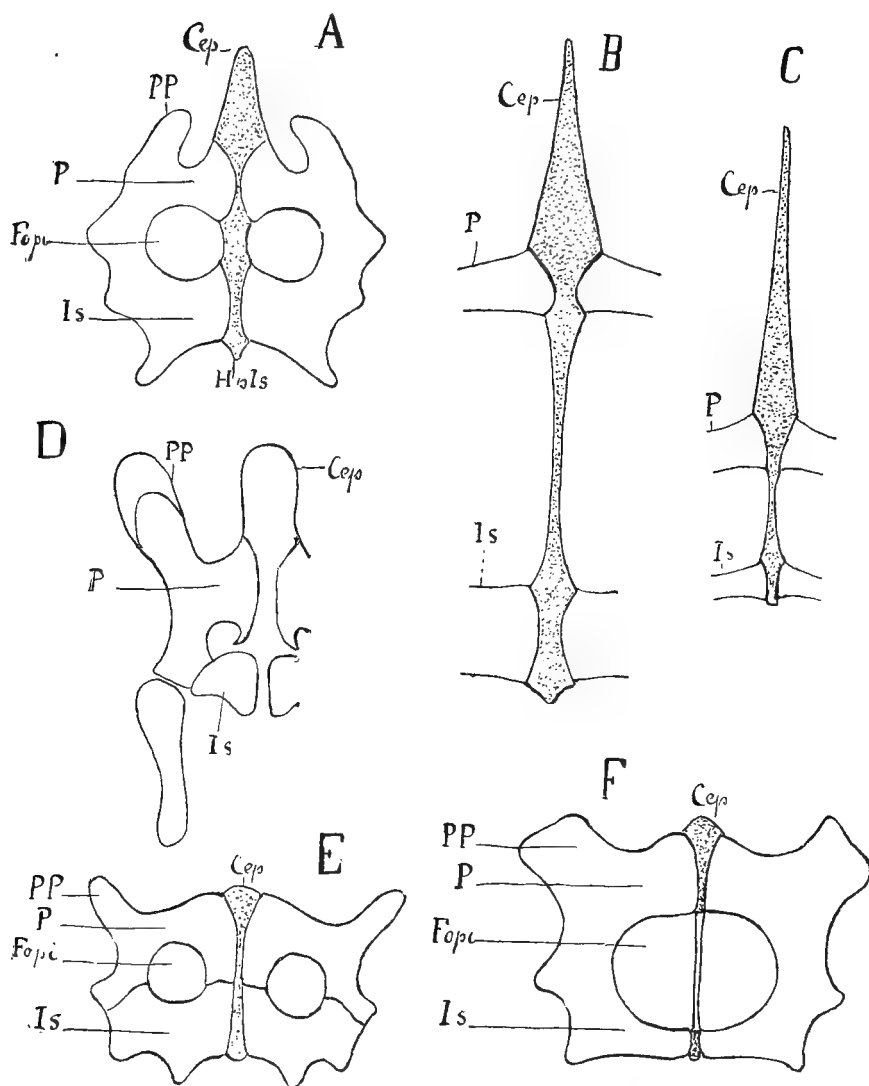
Fig. 94.—Pelvic Arch of Various Chelonians.  (From the ventral side.)  A,
*Macrochelys* (after G. Baur) ; B, median pelvic cartilage of *Chelys fimbriata* ;
C, the same of *Emydura* ; D, *Sphargis coriacea* (after Hoffmann) ; E, *Testudo* ;
F, *Chelone.*

*Cep*, epipubic cartilage ; *HpIs*, hypoischiatic process ; *P*, pubis ; *PP*, prepubis ;
*Is*, ischium ; *Fopi*, ischio-pubic foramen.

compared with that of Amphibians consist in :—(1) a much more
marked differentiation of the pubis, which is more distinctly
separated from the ischium by an ischio-pubic foramen ; (2) the

greater development of the ilium, which is sometimes broadened out at its vertebral end ; and (3) the more intense and solid ossification of the arch as a whole.

Points of connection with the pelvis of Amphibians are seen in Palæohatteria, the Plesiosauria, Hatteria, Telerpeton, and the Chelonia (comp. Figs. 93 and 94), while the pelvis of the Ichthyosauria approaches that of the Lacertilia. In the latter, and still more in the Crocodilia and Dinosauria, the pelvic arch is much
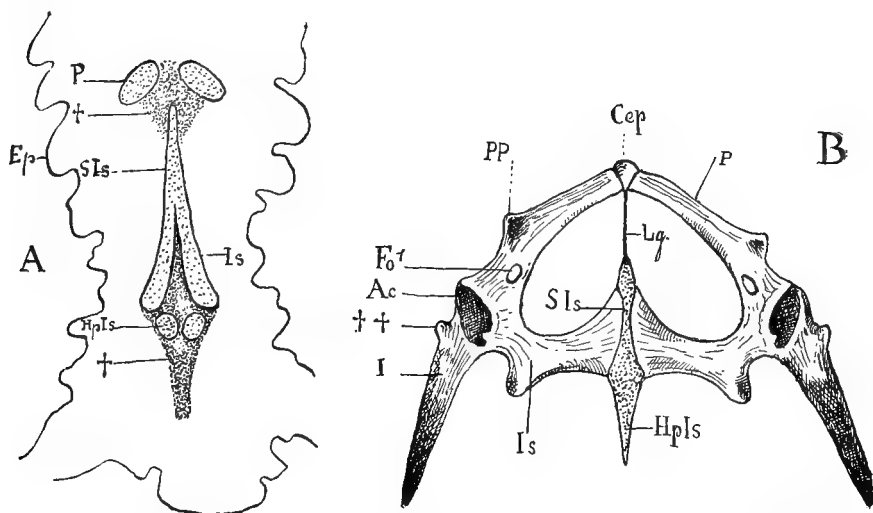


FIG. 95.—A, LONGITUDINAL HORIZONTAL SECTION THROUGH THE VENTRAL PART OF THE PELVIS OF AN EMBRYO OF *Lacerta agilis*, 32 MM. IN LENGTH. B, PELVIS OF *Lacerta vivipara*. (From the ventral side.)

*Ep*, epidermis ; *P*, pubis ; *PP*, prepubis ; *Is*, ischium, forming a symphysis at *SIs* ; *HpIs*, hypoischium, which becomes segmented off from the hinder ends of the ischia in the embryo as a paired structure ; †, dense mass of embryonic tissue ; *I*, ilium, with its small preacetabular process ††, which is much more strongly developed in Crocodiles, Dinosaurians and Birds ; *Ac*, acetabulum, in which the three pelvic bones unite together so that the sutures between them become obliterated ; $Fo^1$, obturator foramen ; *Cep*, epipubis, composed of calcified cartilage ; *Lg*, fibrous ligament.

more highly differentiated ; while in Snakes, on the other hand, it, like the pectoral arch, is entirely wanting.

In *Hatteria* (Fig. 93 E) there is a marked epipubis and a hypoischiatic process continuous with the epipubic cartilage, and the prepubic processes are strongly developed. The obturator and ischiopubic foramina are distinct from one another, and not united into one, as in *Chelonia*. (For the various modifications seen in the pelvis of the latter Order, more particularly as regards the relative development of the epipubic and prepubic processes and the relations of the ischium and pubis, compare Fig. 94.)

The pelvis of the typical *Lacertilia* (Fig. 95 B) is characterised by a lightness of build. The rod-like pubis and ischium are separated from one another by large ischiopubic foramina, and between them in the middle line is a longitudinal fibro-cartilaginous ligament, continuous anteriorly with the plug-like epipubic cartilage and posteriorly with the hypoischium. This tract represents the
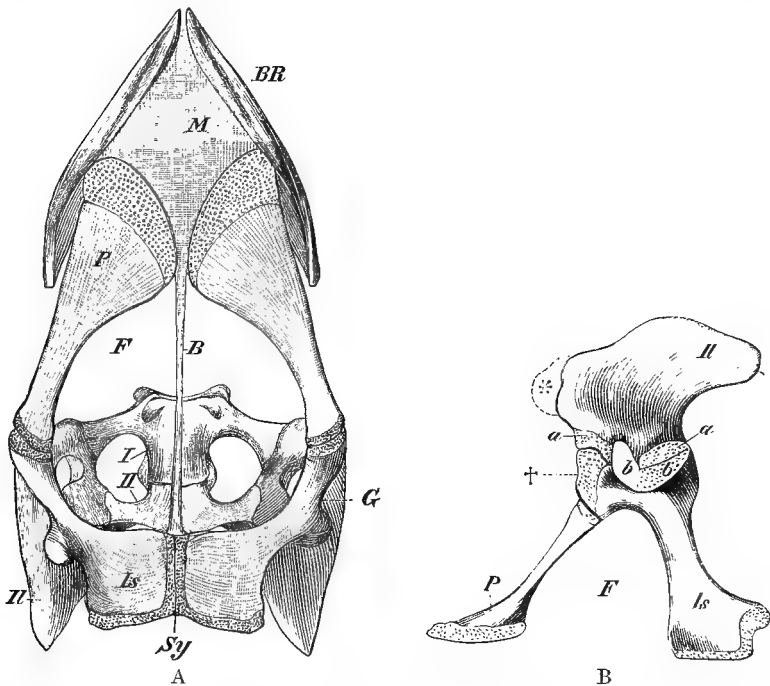


FIG. 96.—PELVIS OF A YOUNG *Alligator lucius.* (A, ventral, and B, side view.)

*Il*, ilium ; *Is*, ischium ; *P*, pubis ; *Sy*, symphysis of ischium ; *F*, ischio-pubic foramen ; *B*, fibrous band between the symphyses pubis and ischii ; †, pars acetabularis, which is interposed between the process *a* of the ilium and the pubis ; *b*, foramen in the acetabulum, bounded posteriorly by the two processes, *a* and *b*, of the ilium and ischium respectively ; *, indication of a forward growth of the ilium, such as is met with in Dinosaurians and Birds ; *G*, acetabulum ; *I, II*, first and second sacral vertebræ ; *M*, fibrous membrane extending between the anterior margin of the pubis and the last pair of "abdominal ribs" (*BR*.)

remnant of the median ends of the pubis and ischium which are present in the embryo (Fig. 95 A) ; and thus in this, as in certain other respects, the pelvis of the Lacertilia may be said to pass through a Hatteria-like stage in the course of development. The epipubis and hypoischium arise as paired rudiments. The ilium in some cases is almost vertical in position : in others it is

more oblique, sloping upwards and backwards from the acetabulum.

The pelvis of *Crocodiles* exhibits special characteristics and is of particular interest, as in some points it resembles that of certain extinct forms. The pubes, which have at first a transverse position, become later directed forwards much more markedly than in Chelonians and Lizards, and thus the ischiopubic foramina (in which the obturator foramina are included) are very wide, and are separated from one another by a fibrous cord (Fig. 96). A symphysis, both of the pubis and ischium, is formed, but the former is not present in the adult. The acetabulum is perforated, and the pubis is separated from it by a cartilaginous *pars acetabularis*, not represented in lower Vertebrates, formed from the acetabular process of the ilium. The epipubis is possibly represented by a cartilaginous apophysis at the anterior (distal) end of the pubis, but it never becomes separately differentiated.

The ilium becomes greatly broadened out in the antero-posterior direction dorsally, where it is attached to the sacrum ; and this is of special interest as a similar extension of the ilium occurs still more markedly in Dinosaurians and Birds (Fig. 97).

**Birds.**—The pelvis of Birds is chiefly characterised by the relatively large development of the iliac region and by the position of the delicate pubis, which in the course of development becomes
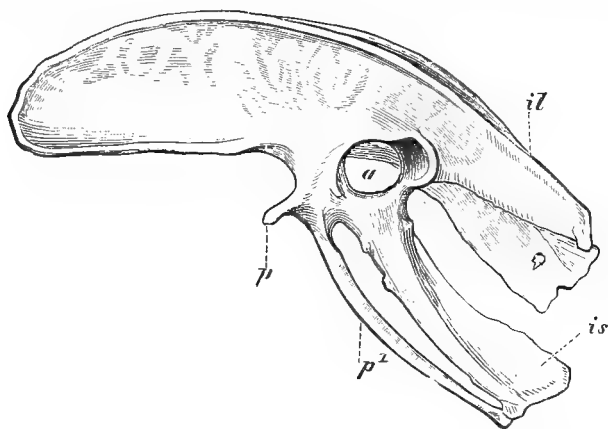


FIG. 97.—PELVIS OF *Apteryx australis*. Lateral view. (After Marsh.)

*il*, ilium ; *is*, ischium ; *p*, spinous process from the pars acetabularis ; $p^1$, pubis ; *a*, acetabulum.

directed backwards, parallel to the ischium and post-acetabular process of the ilium, and is often united with the ischium

(Carinatæ). The preacetabular portion of the ilium extends forward for a considerable distance, and a number of vertebræ belonging to other than the true sacral region become secondarily connected with the ilium (*see* p. 48). The acetabulum is perforated, and the pars acetabularis (p. 119) forms a spinous process. The elements of the pelvis usually become anchylosed together. The pubis meets its fellow in the middle line only in Struthio, and the ischium only in Rhea.

**Mammals.**—The elements of the pelvis here remain separated for a long time by cartilage, but later they become fused together. The pubis always takes less part in the formation of the acetabulum than do the other two bones, and may be more or less entirely shut out from it by an ossification of the pars acetabularis, which subsequently unites with either the ilium, ischium, or pubis (Figs. 98 and 99). This *acetabular bone* is especially well developed in the Mole, in which it shuts the ilium, as well as the pubis, out of the acetabulum : the latter is perforated in Monotremes. The angle between the axes of the ilium and sacrum is large in Ornithorhynchus, and more acute in other Mammals.

The original type with both pubic and ischiatic symphyses is seen in Monotremes, Marsupials (Fig. 100), many Rodents, Insectivores and Ungulates. In many other Insectivores, in Carnivores, and more particularly in the Primates, the ischia no longer meet below. The greatest amount of variety in the form of the pelvis
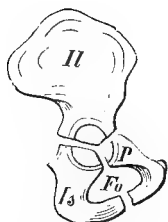


FIG. 98.—EXTERNAL VIEW OF THE RIGHT HALF OF THE HUMAN PELVIS. (From the outer side.)

The three bones—ilium (*Il*), ischium (*Is*), and pubis (*P*)—are shown distinct from one another in the acetabulum. *Fo*, obturator foramen.
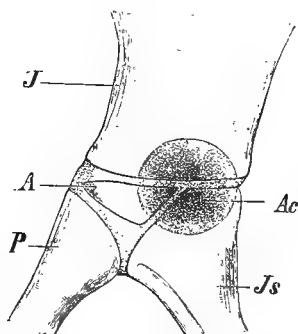
FIG. 99.—DIAGRAM SHOWING THE RELATIONS OF THE PARS ACETABULARIS (in *Viverra civetta*).

*J*, ilium ; *Js*, ischium ; *P*, pubis ; *A*, acetabular bone ; *Ac*, acetabulum.

in any one order is seen in Insectivores, in some of which (*e.g.*, Mole), as well as in most Bats, there is no symphysis pubis. The obturator foramen is always surrounded by bone.

In Whales, in which hind-limbs are wanting, paired rudiments of the ischio-pubic region of the pelvis are present. They are unconnected with one another and with the vertebral column.

In Monotremes and Marsupials of both sexes, two strong so-called "marsupial bones" (Fig. 100) arise from the anterior border of the pubes, right and left of the middle line, and extend forward in a straight or oblique direction embedded in the
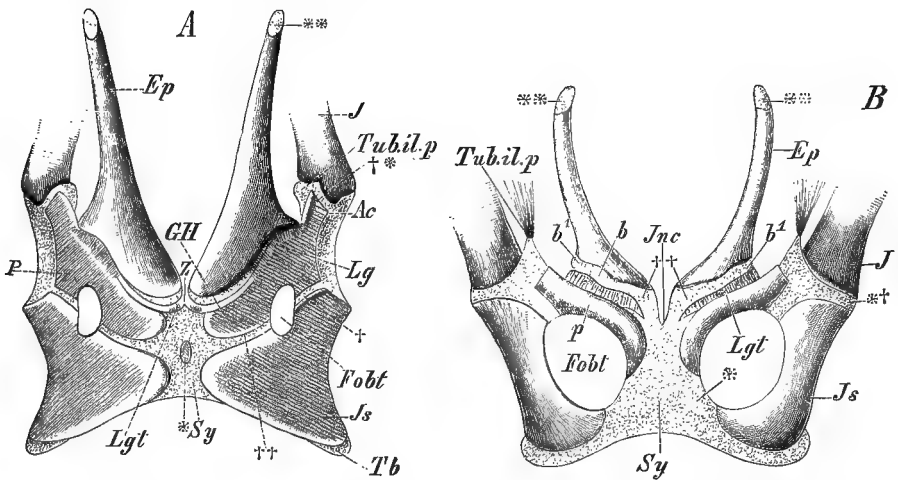


FIG. 100.—PELVIS OF A, *Echidna hystrix* (ADULT), AND B, *Didelphys azaræ* (FŒTUS, 5·5 CM IN LENGTH). (From the ventral side.)

*Ep*, epipubis ("marsupial bone") ; *P*, pubis ; *Sy*, ischiopubic symphysis ; *Js*, ischium ; *J*, ilium ; *Fobt*, obturator foramen ; *Tub.il.p*, ilio-pectineal tubercle ; *Lg* and *Lgt*, ligament between the pubis and epipubis ; **, cartilaginous apophysis at the anterior end of the epipubis.

In Fig. A, †*, †, ††, ilio- and ischio-pubic sutures ; *Z*, process on the anterior border of the pubis ; *GH*, articulation between the pubis and epipubis ; *Tb*, cartilaginous tuber ischii.

In Fig. B, *b*, *b¹*, cartilaginous base of the epipubis, continuous with the inter-pubic cartilage at † ; *, *†, ischio-pubic and ischio-iliac suture.

body-walls. They form an integral part of the pelvis, and in the embryo are seen to be in direct connection with its cartilaginous symphysis ; but later on articulations are formed between them and the pubes. There can be no doubt that these structures are the homologues of the epipubis of lower Vertebrates, which has been retained in non-placental Mammals in order to serve as a support for the abdominal walls in connection with the marsupial pouch (p. 28).

FREE LIMBS.

## Fishes and Dipnoans.

In the following description the pelvic fin will be considered before the pectoral, as it usually retains a simpler and more primitive form.

*Elasmobranchii and Holocephali.*—The cartilaginous skeleton of the fins is the most richly segmented in these Fishes.   There are usually two main elements (basalia) in the pelvic fin which articulate with the arch and with which a variable number of segmented rays (radii) are connected, the latter passing towards the periphery of the fin (Fig. 88). Both the larger, posterior main element (*basi-* or *metapterygium*), and the smaller, inconstant *propterygium* must, as already stated (p. 105), be looked upon as originating—phylogenetically, at any rate—by a fusion of the proximal ends of the primary cartilaginous rays of the fin; and the form and relations of these main elements vary according to the degree in which such a fusion has taken place.[1]  This is also true as regards the pectoral fin, in which an additional basal piece, or *mesoptery-gium*, is usually present between the pro- and metapterygia, and, like these, articulates with a special convexity on the pectoral arch (Fig. 83) : there may even be four basalia.   These complications arise in connection with the greater importance of the pectoral than the pelvic fin as an organ of locomotion. The distal portions of both fins are supported by horny fibres (p. 103). With the exception of one (Fig. 83, †)— or at most of very few—all the rays are situated on the same side of the basalia (*uniserial* type).
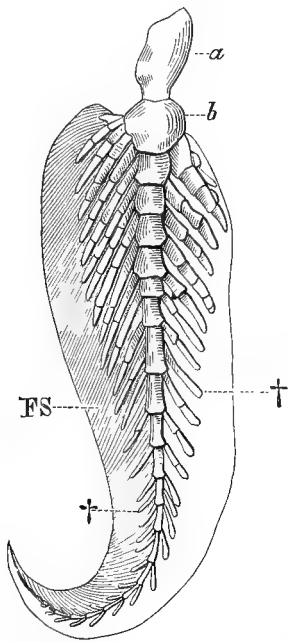


FIG. 101.—PECTORAL FIN OF *Ceratodus fosteri.*

*a, b,* the two first segments of the main axial ray ; †, †, lateral rays ;  *FS,* horny rays, shown only on one side.

*Dipnoi.*—The cartilaginous pectoral and pelvic fins are here also essentially similar to one another, the latter being rather the simpler of the two.   From a segmented main-ray or

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[1] In male Elasmobranchii and Holocephali a number of pieces of cartilage are connected with the distal end of the metapterygium of the pelvic fin as a support for the copulatory organs or claspers : these may become more or less calcified.

axis a number of segmented secondary rays arise on either side in
Ceratodus : these are not, however, strictly symmetrical (Fig. 101).
Beyond them horny rays are present, as in Elasmobranchs. A
proximal (basal) segment of the axis, which bears no rays, articu-
lates with the arch. In Protopterus and Lepidosiren the fins, with
their skeleton, have undergone a marked reduction, so that little
more than the segmented axis remains.

Thus the fins of Dipnoans differ from those of Elasmobranchs
(as well as of Ganoids and Teleosts) in being formed on a *biserial*
type.

*Ganoidei.*—The skeleton of the fin is much simpler and the
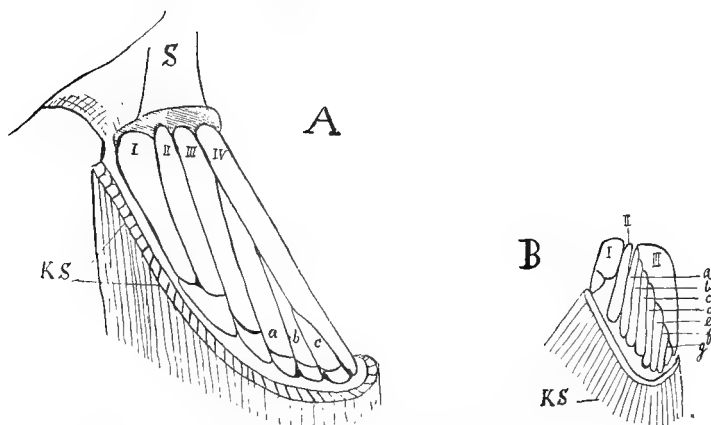


Fig. 102. —Left Pectoral Fin of A, *Polyodon (Spatularia)*, and B, *Amia*.

*I-IV*, cartilaginous radii connected with the arch (*S*) ; *a-g*, radii which do not
reach the arch and are connected with the most posterior ray (*IV* in *A*, *III*
in B) ; *KS*, bony rays.

primary rays much fewer in number in Ganoids than in Elasmo-
branchs.

In the pelvic fin of cartilaginous Ganoids more or fewer of the
radii unite together proximally to form a basale, which is perforated
by nerves, and from which a very primitive pelvic plate becomes
differentiated (p. 109, Fig. 87, B). It is important to bear in mind
that the distinction between an axis and secondary rays cannot
here, therefore, be strictly recognised, and the fin is thus more
primitive than in Elasmobranchs.

The primitive relations have to a certain extent disappeared in
the pectoral fin of cartilaginous Ganoids, which, however, consists
of a varied number of rays. Of these, four reach the arch in
Polyodon (Fig. 102, A) and five in Acipenser.

In the pectoral fin of Amia (Fig. 102, B) two large converging
marginal rays articulate with the shoulder-girdle, and only one

intermediate ray reaches the arch : this condition may be compared with that seen in the highly-developed pectoral fin of Polypterus (comp. Fig. 103).

The form of the pelvic fin in bony Ganoids may be easily derived from that seen in the cartilaginous representatives of this Order, but the number of radii is greatly reduced (Fig. 87). The rays supporting the distal part of both pairs of fins are bony (comp. p. 103).

*Teleostei.*—A still further reduction has taken place in the primitive skeleton of the paired fins in Teleosts, there being at most only a few radials articulating with the arch (Fig. 84), and even these (especially in the case of the pelvic fin) may be wanting. The main part of each fin is supported by bony rays, as in osseous Ganoids. The skeleton of the fins of Siluroids, Cyprinoids, and Gymnotidæ comes nearest to that of Ganoids.



FIG. 103.—PECTORAL FIN OF
*Polypterus.*

*Pr, Ms, Mt,* pro-, meso-, and metapterygium, the first and last mentioned meeting at †, so that the mesopterygium does not reach the arch ; *OSS*, centre of ossification in *MS* ; * part of the mesopterygium which extends between the distal end of the propterygium and the first row of radii ; *Nl*, nerve foramina in the mesopterygium ; *Ra, Ra¹*, radii ; *FS*, bony dermal rays.

### Phylogeny of the Ichthyopterygium.

Two essentially different views exist as to the primitive form of fin-skeleton in Fishes. As already mentioned on p. 106, Gegenbaur postulates a *biserial* fin as the primitive type (archipterygium), which is most clearly retained in Ceratodus. He supposes that the uniserial form has been derived from this by a reduction of the rays on one side and a further development of those on the other. The axial ray of the biserial fin would thus correspond to the basi- or metapterygium, while the pro- and mesopterygia of the uniserial fin would answer to special developments of the proximal ends of certain of the rays on one side of it.

The other view, which seems a far more probable one, is that the *uniserial* type is the more primitive, and that this type is most nearly retained in Elasmobranchs, which are as ancient a group as the Dipnoans and which have not passed through a Dipnoan stage in the course of their phylogenetic development.

Fig. 82 represents the mode of origin of the Elasmobranch fin

in accordance with this view, which is further supported by many
of the facts stated above and by numerous others relating to the
structure and development of the fins in Fishes, as well as by a
study of such fossil forms as the Palæozoic Cladoselache.

<p style="text-align:center">GENERAL CONSIDERATIONS ON THE LIMBS OF THE<br>HIGHER VERTEBRATA.</p>

It thus appears possible to derive the skeleton of the fin of all
the orders of Fishes from a single ground-type, but to trace the con-
nection of the latter with the extremities of Amphibia and Amniota
is a far more difficult task. Between these two types of limb there
seems to be a wide gap, in consequence of the different conditions
of life existing between aquatic and terrestrial Vertebrates : we do
not know how the limb of an air-
breathing Vertebrate (*cheiroptery-
gium*), adapted for progression upon
land, has been derived from the fin
(*ichthyopterygium*), only fitted for use
in the water.

Palæontology furnishes no answer
to this question ; we know of no
fossil intermediate forms of limb,
and the various hypotheses which
have been put forward on the sub-
ject cannot be discussed here. We
may suppose that when the primitive
Amphibian first began to take on a
terrestrial mode of life, its fin, which
is practically a single-jointed lever,
amply sufficient for the movement of
the body in a fluid medium, became
gradually transformed into a many-
jointed system of levers.



Fig. 104.—DIAGRAMMATIC FIGURES
TO SHOW THE RELATIONS OF THE
ANTERIOR FREE EXTREMITY TO
THE TRUNK IN FISHES (A), AND
THE HIGHER VERTEBRATES (B).

*S*, pectoral arch ; *Mt*, metaptery-
gium ; *Rd*, radialia in A, radius
in B ; *Ul*, ulna ; proximally to
*Ul* and *Rd* is the humerus.

In other words, as the function of the limb was no longer
simply to propel the body, but also to lift it up from the
ground, the firmly-connected elements of the skeleton of the
fin gradually became loosened from, and placed at an angle
to, one another (knee, elbow), definite articulations being
formed between them in a proximo-distal direction. Moreover,
the extremity must have changed its position with regard to the
body, so that, instead of projecting horizontally outwards, it became
bent downwards, and thus the angle between it and the median
plane of the trunk was gradually reduced, until in Mammals even-
tually, the longitudinal axis of the limb, when at rest, came to lie
parallel with the median plane of the body. In the higher types
this is more particularly the case as regards the posterior ex-

tremities, the anterior undergoing the most varied adaptative modifications, and giving rise to tactile, prehensile, or flying organs —or, as in aquatic Mammals, becoming once more converted into rowing organs. The limbs of all the higher Vertebrata may, however, also be reduced to a single ground-type.

The fore- and hind-limbs show a great similarity as regards the form and position of their various parts. A division into four principal sections can always be recognised: in the case of the fore-limb these are spoken of as upper arm (*brachium*), fore-arm (*antibrachium*), wrist (*carpus*), and hand (*manus*); and in the hind-limb as thigh (*femur*), shank (*crus*), ankle (*tarsus*), and foot (*pes*) (Figs. 105, 106). The bone of the upper arm (*humerus*) and of the thigh (*femur*) is always unpaired, but two bones are present in the fore-arm and shank. The former are called *radius* and *ulna*, and the latter *tibia* and *fibula*. The hand and foot are also respectively divisible into two sections, a proximal *metacarpus* and *metatarsus*, and a distal series of *phalanges*, which form the skeleton of the fingers and toes (*digits*).



FIG. 105.—SKELETON OF THE RIGHT FORE-ARM, CARPUS, AND HAND OF *Salamandra maculosa*. (From above.)

*R*, radius; *U*, ulna; *r*, radiale; *i*, *u*, intermedio-ulnare; *c*, centrale; 1 to 4, first to fourth carpalia (according to Emery, 1 corresponds to the carpal of the prepollex, and 2 to the common carpal of digits *I* and *II*); *Mc*, *Mc*, metacarpals; *Ph*, phalanges; *I* to *IV*, first to fourth fingers.

Both manus and pes are made up of several series of cylindrical bones. There are never more than five complete series, which—except as regards number—present essentially similar primary relations throughout the higher Vertebrates. The skeleton of the carpus and tarsus, each of which always consists of a series of small cartilages or bones, shows much variation; but the following may be taken as a ground-type (Figs. 105 and 106). Round a *centrale*, which may be double, is arranged a series of other elements, of which three are proximal, and a varying number (four to six) distal. The proximal, in correspondence with their relations to the bones of the fore-arm and shank respectively, are spoken of as *radiale* or *tibiale*, *ulnare* or *fibulare*, and *intermedium*; while the

distal are called *carpalia* or *tarsalia* (in the narrower sense). They are counted beginning from the pre-axial (radial or tibial) side of the limb.

**Amphibia.**—The anterior and posterior extremities of Urodela are formed essentially on the ground-plan described above. There are usually five digits in the hind-limb, and always four in the fore-limb. In the Anura the radius and ulna become fused together, and a separate intermedium is wanting; the proximal row of the tarsus, moreover, consists of only two cylindrical bones, one of which (*astragalus*) corresponds to a tibiale, and the other (*calcaneum*) to a fibulare.[1]

In the distal row of the carpus four separate elements are formed, but this number may become reduced owing to secondary fusions; in rare cases a fifth carpal may also be present. Very different views exist as regards the homologies of the individual carpals of Anurans. In the distal row of the tarsus, tarsalia *II* and *III* are the most constant elements, but even these may undergo fusion; tarsalia *IV* and *V* are generally represented by a ligament; and tarsale *I* usually does not long remain distinct.

In Anura the metatarsals and phalanges, between which the web of the foot is stretched, are very long and slender. The femur, as well as the bones of the shank, which are fused together, are also exceedingly long, in correspondence with the mode of progression of these animals. The skeleton of the extremities is more strongly ossified in Anurans than in Urodeles, in which many of the elements remain cartilaginous.



FIG. 106.—SKELETON OF THE SHANK, TARSUS, AND FOOT OF *Spelerpes fuscus*.

*tb*, tibia; *fb*, fibula; *t*, tibiale; *i*, intermedium; *f*, fibulare; *c*, centrale; 1-5, tarsalia; *i-r*, digits.

Traces of an extra toe (*prehallux*) occur on the tibial side of the tarsus, and in both Urodeles and Anurans indications of an additional pre-axial digit in the manus are occasionally met with. The number of phalanges on the individual digits varies in different Amphibians.

Rudiments of the extremities can be recognised externally in embryos of the limbless Gymnophiona.

**Reptiles.**—Chelonians and Lizards (and more especially Hat-

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[1] It is possible that the tibiale and fibulare also include the representatives of other elements.

teria) [1] closely resemble Urodeles in the structure of the carpus, although the exact homologies of all the different elements cannot yet be stated with certainty. Five digits are always present in both manus and pes, and in Chelonians traces also of the former possession of an extra finger both on the radial and ulnar side (" pisiform ") are to be seen (Figs. 107, 108, and 109). The tibia and fibula always remain separate.

In Crocodiles, which, like Anurans, possess no trace of an intermedium, the proximal row of the carpus consists of two hourglass-shaped bones—a larger radiale, and a smaller ulnare (Fig. 110). A rudiment of a sixth ray is present on the outer side of
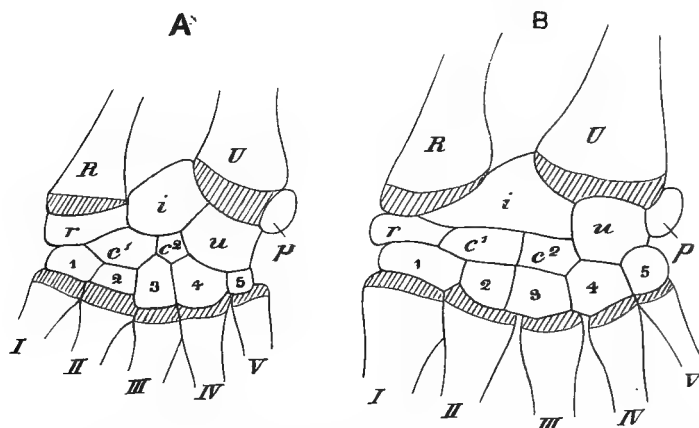


FIG. 107.—CARPUS OF A, *Hatteria (Sphenodon) punctata*, AND B, *Emydura krefftii*. (After Baur.)

$R$, radius ; $U$, ulna ; $r$, radiale ; $u$, ulnare ; $i$, intermedium ; $c^1$, radial centrale ; $c^2$, ulnar centrale ; 1-5, carpalia ; $p$, ulnar sesamoid (pisiform); $I$-$V$, the metacarpals.

the latter. The centrale, as in Anura, comes to be situated in the distal row, which is much less developed than the proximal.

In all Reptiles the tarsus undergoes a marked reduction, especially in its proximal portion, and gradually leads to the type seen in Birds. Thus in Chelonians and Lizards the proximal tarsals all run together into a single mass which corresponds to the tibiale, intermedium, fibulare, and centrale, and the last mentioned element can no longer be recognised in Lizards, even in the embryo. Traces of an extra radial ray are present.

In the distal row three or four (five in Palæohatteria) separate tarsals are developed, but these may unite partly with one another

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[1] In Hatteria and Chelydra serpentina amongst existing Reptiles, a double centrale is present in the carpus, and traces of a double condition of this element are seen in certain other Chelonians.

(Chelonians), and partly with the corresponding metatarsals (Lizards); thus there is an increasing tendency for the movement of the foot to take place by means of an *intertarsal* articulation, as in Birds.

In Crocodiles there are two bones in the proximal row of the tarsus, one of which corresponds to a tibiale, intermedium, and centrale, the other to a fibulare. The former is spoken of as the astragalus, the latter as the calcaneum, and on it a definite heel (*calcaneal process*) is seen for the first time in the animal series.
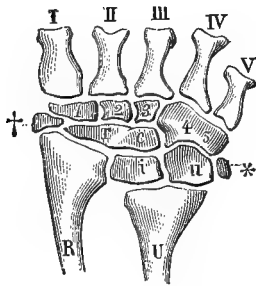


FIG. 108.—RIGHT CARPUS OF *Emys europæa*. (From above.)

*R*, Radius; *U*, ulna; *r.c,* fused radiale and centrale (or centrale 1 and 2, Baur); *i*, intermedium; *u*, ulnare; 1-5, the carpalia, of which 4 and 5 have become fused together; † (radiale, Baur) and *, elements on the radial and ulnar side respectively, indications of additional radial and ulnar (pisiform) rays; *I-V*, the metacarpals.
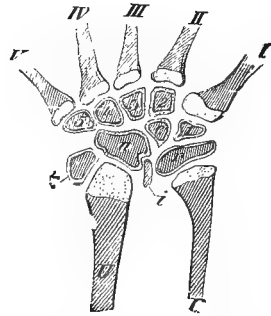
FIG. 109.—LEFT CARPUS OF *Lacerta agilis*. (From above.)

*R*, radius; *U*, ulna; *u*, ulnare; *i*, intermedium; *r*, radiale, formed by the fusion of two elements, one of which corresponds to a prepollex; *c*, centrale; 1-5; carpalia; †, ulna sesamoid (pisiform); *I-V*, the metacarpals.

The distal row consists originally of four small cartilages, but these later undergo a partial fusion.

The number of phalanges on the fourth and fifth digits in the manus is greater in the embryos of Crocodiles than in the adult. This indicates that the Crocodilia have been derived from forms possessing a fin-like fore-limb.

In Ichthyosaurus and Plesiosaurus the limbs are modified to form paddles, the digits consisting of numerous phalanges, and additional rays being present in the former genus. In Pterodactylus and Rhamphorhynchus the fourth finger was produced into a long jointed rod, which supported a wing-like expansion of the integument.

Amongst the Lacertilia, various degrees of reduction of the extremities may occur, and in certain Snakes (*e.g.*, Python) traces of the hind-limbs exist.

**Birds.**—The fore-limb of Birds is considerably modified by adaptation for flight. The manus loses its primitive character and undergoes reduction, while the brachium and antibrachium, as

well as the entire pectoral arch and sternum, are extraordinarily developed.    In the Ratitæ, however, the wing has undergone regressive changes in connection with the habits of these Birds.

Of the six or seven carpals which may be present in the embryo, the three distal become fused with the corresponding metacarpals, thus forming a *carpometacarpus* (Figs. 111, 112 *A*), and in the adult only the two proximal remain separate as a radiale and an ulnare.    The three metacarpals themselves become united together proximally, and the second and third distally : they only bear a very limited number of phalanges at their free ends.



*Claws* were present on the terminal phalanges of all three digits in Archæopteryx.    In certain recent Birds the first digit bears a claw, and more rarely the second and even the third also.

The tarsus is still more reduced in Birds than in Reptiles, and consists in the embryo of three elements, two small proximal and a broader distal.    The former (tibiale and fibulare) unite later with the distal end of the tibia, thus forming a *tibiotarsus*, while the latter, which corresponds to tarsalia *I* to *V*, becomes included in the base of the metatarsus.    Thus the foot of adult Birds no longer possesses any distinct tarsal elements, though, as in Chelonians and Lizards, the foot really moves by an intertarsal articulation.    Of the original five metatarsals, the fifth soon disappears, while the second, third, and fourth become united with one another and with the distal element of the tarsus to form a single bone, the *tarsometatarsus* (Figs. 111, 112 B).    The first metatarsal remains to a greater or less extent independent.

FIG. 110.—RIGHT CAR-
PUS OF A YOUNG
*Alligator      lucius.*
(From above.)

*R*, radius ; *U*, ulna ; *r*, radiale (including, according to Emery, a carpal of the prepollex) ; *u*, ulnare ; *C*, centrale ; 1 to 5, the five carpalia, as yet unossified, of which 1 and 2, as well as 3, 4, and 5, have become fused together ; †, pisiform ; *I* to *V*, the metacarpals.

The number of toes varies between two (Struthio) and four ; that of the phalanges is normally 2, 3, 4, 5, reckoning from the first to the fourth digit.    The tibia, even from the first, greatly exceeds the fibula in size, and the two bones become fused together distally.

In both limbs the bones are usually pneumatic. (*See* under *Air-sacs*.)

**Mammals.**—In Mammals the anterior extremity either remains in the condition of a simple organ of locomotion, serving for progression on land ; or it may become modified in adaption to an

aërial (Bats) or aquatic (Pinnipedia, Cetacea, Sirenia) mode of life ; or, again, it may give rise to a prehensile organ. In the latter case (Primates) the radius and ulna, instead of being firmly connected together, articulate with one another, the former being capable
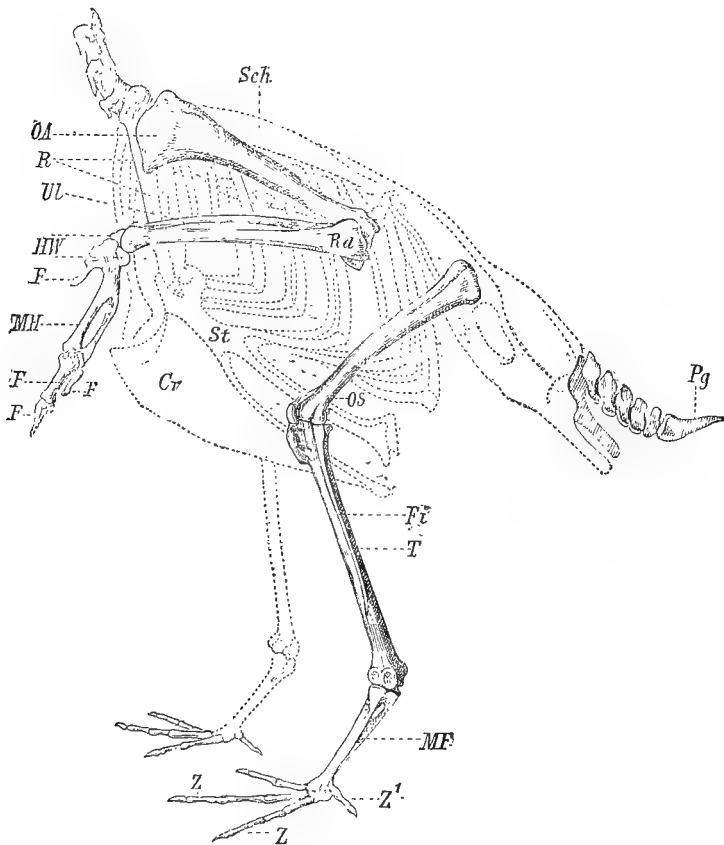
FIG. 111.—SKELETON OF THE LIMBS AND TAIL OF A CARINATE BIRD. (The skeleton of the body is indicated by dotted lines.)

*Sch*, scapula ; *R*, coracoid ; *St*, sternum, with its keel (*Cr*) ; *OA*, humerus ; *Rd*, ulna ; *Ul*, radius ; *HW*, carpus ; *MH*, carpometacarpus ; *F*, digits ; *OS*, femur ; *T*, tibiotarsus ; *Fi*, fibula ; *MF*, tarsometatarsus ; $Z^1$, $Z$, digits ; *Py*, pygostyle.

of rotation round the latter : thus the manus can be brought into a position of *pronation* or of *supination*.

The tibia is the most important bone of the shank, and the fibula often becomes fused with it to a greater or less extent ; the ulna also may unite with the radius. Except in the Cetacea,

Sirenia, Cheiroptera, and certain Marsupialia, a sesamoid bone is developed in the distal tendons of the great extensor muscles of the shank, and is known as the knee-cap or *patella*. This is already present in certain Lizards and in Birds.

The carpus and tarsus most nearly correspond with those of Urodeles and Chelonians, and, as in them, certain of the elements
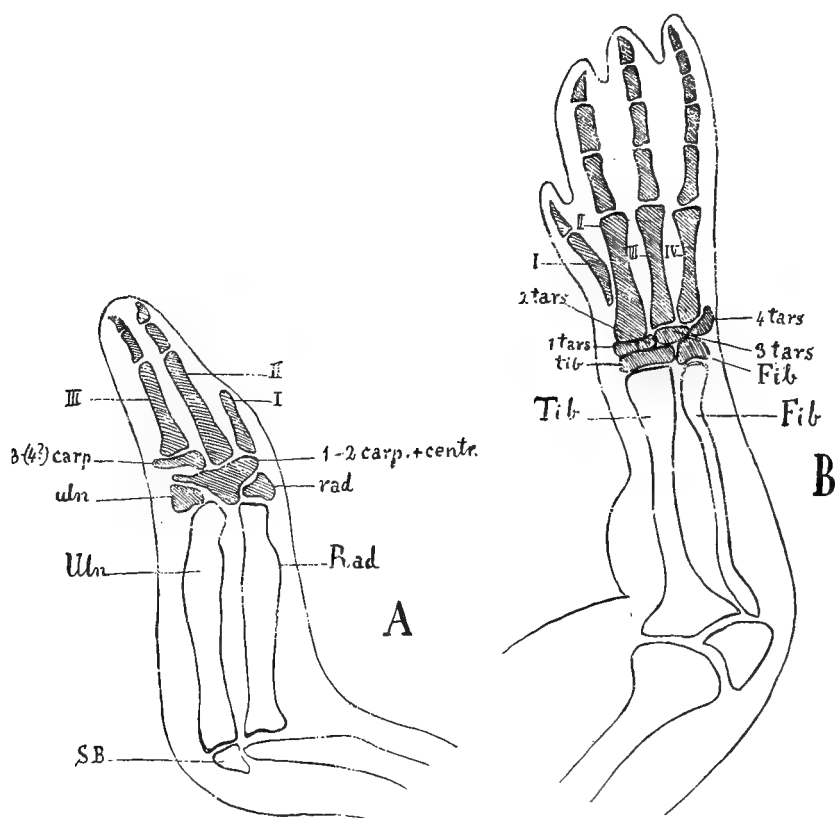


FIG. 112.—A. FORE-ARM AND MANUS OF EMBRYO PENGUIN (*Eudyptes chrysocome*). (Fourteenth day of incubation.) (After Th. Studer.) (*SB* is a sesamoid developed in the tendon of the triceps in this Bird.) B. SHANK AND FOOT OF EMBRYO PENGUIN. (At the same stage.)

may become fused together. Thus the intermedium and tibiale as a rule unite to form an astragalus, while the fourth and fifth carpals become fused to form the so-called *unciform bone*, and the corresponding tarsals give rise to the *cuboid*. A centrale, varying much in form and size, is usually present at an early stage in all five-fingered Mammals, but as a rule it becomes fused later with one, or with two, of the neighbouring carpals—generally the

radiale (*e.g.*, the Gorilla, the Chimpanzee, and Man, though it may persist in the human subject throughout life or may fuse with carpale 2 or 3). In the tarsus the centrale (*navicular*) remains distinct, and usually lies on the inner border of the foot.

So much difference of opinion exists with regard to the homologies of the bones of the carpus and tarsus in Mammals, that it is not possible at present to give a satisfactory account of them, or of the additional elements which are often present in the embryo and disappear during development. Thus the pisiform may be a true sesamoid, or may represent an additional ulnar ray, and the calcaneum may or may not be the complete serial homologue of the pisiform. Elements occur occasionally in the carpus and tarsus which are supposed to represent additional radial and tibial rays respectively—the so-called *prepollex* and *prehallux* (Fig. 113).

There are typically five complete digits on each foot, but this number may be reduced to four, three, or even one (Figs. 114 and
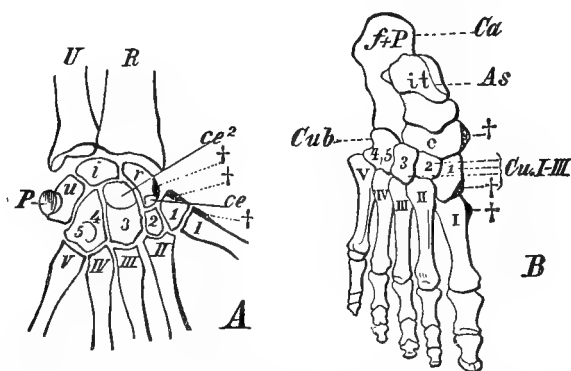


FIG. 113.—A, CARPUS, AND B, SKELETON OF THE FOOT OF MAN. (The rudiments of the so-called prepollex and prehallux (†††) are represented diagrammatically.

*U*, ulna ; *R*, radius ; *r*, radiale ; *i*, intermedium ; *u*, ulnare ; *P*, pisiform ; *ce*, centrale, fused with the radiale ; *ce²*, second centrale, forming the head of tarsale 3 ; 1-5, the carpalia and tarsalia, 4 and 5 being united to form the unciform and cuboid respectively ; *Cu I-III*, the first to third tarsalia ; *c*, centrale tarsi (navicular) ; *it*, intermedio-tibiale = astragalus (*As*); *f + p*, calcaneum (= fibulare and pisiform tarsi ?) ; *I-V*, the metacarpals and metatarsals.

115), the disappearance taking place in the following order— 1, 5, 2, 4 : thus in the horse the third is the only complete digit remaining (Fig. 115). The number of phalanges is similar in both hand and foot: in the first digit there are only two, while in the others there are three. An exception to this rule is seen in Cetacea, in which the phalanges are numerous, as in Ichthyosaurus and Plesiosaurus amongst Reptiles.

It is interesting to trace the reduction which has taken place in the feet of Ungulates in the course of time. Fig. 115 represents successive stages in the

phylogenetic development of the fore-foot of the Horse, showing how it has been gradually derived from a tetra- or pentadactyle form; and it has recently been ascertained that all these stages are passed through in the course of ontogeny. In this case the third digit becomes greatly enlarged relatively (*perissodactyle form*), and eventually is the only one remaining, while in cloven-footed Ungulates the third and fourth digits are both functional and equally strongly developed (*artiodactyle form*) and may be united together to form a "cannon-bone," the others becoming gradually reduced. A similar reduction takes place in the hind-foot, and is here as a rule more rapid.



FIG. 114.—SKELETON OF THE LEFT FORE-LIMB OF *A*, PIG; *B*, HYOMOSCHUS; *C*, TRAGULUS; *D*, ROEBUCK; *E*, SHEEP; *F*, CAMEL. (From Bell, after Garrod.)

Ungulates diverged into Artiodactyles and Perissodactyles as far back as the Eocene period, but a large series of Tertiary forms shows that they must all have been derived from a common pentadactyle ancestral form.

Some of the many other adaptive modifications of the limbs in Mammals must also be briefly mentioned. In Bats, the phalanges are greatly elongated to support the wing-membrane ; the hallux as well as the pollex may be opposable amongst the Primates ; the fore-limbs are modified for digging in certain Mammals (*e.g.* Mole) ; and in the Cetacea (*see* p. 133) and Sirenia the digits are not free, and serve as supports for the fin-like paddles. Nails are present on the digits of Sirenia, but have disappeared in the Cetacea, though they can still be recognised in the embryo of toothed Whales. Hind-limbs are absent



FIG. 115.—FORE-FOOT OF ANCESTRAL FORMS OF THE HORSE. 1. OROHIPPUS (Eocene). 2. MESOHIPPUS (Upper Eocene). 3. MIOHIPPUS (Miocene). 4. PROTOHIPPUS (Upper Pliocene). 5. PLIOHIPPUS (Uppermost Pliocene). 6. EQUUS.

in the two last mentioned Orders, but indications of them can be seen even externally in very young embryos of the Porpoise, and rudiments of the thigh and even shank bones occur in the adult in certain Whales (comp. p. 121).

# C. MUSCULAR SYSTEM.

THE muscles, commonly spoken of as flesh, may be divided into two groups, according to the histological character of their elements, which consist of cells elongated to form contractile *fibres*: namely, into those with *smooth* and those with *transversely-striated* fibres. The former are phylogenetically the older, and are to be looked upon as the precursors of the latter. The action of both in causing movements is dependent on the nervous system.

The smooth or *involuntary* muscle-fibres preponderate in the vascular system, viscera, and dermis, and are not under the control of the will; almost all the striated or *voluntary* muscles occur in the body-walls and organs of locomotion, and are under the control of the will.[1] The following general statements refer exclusively to the latter kind of muscles, which may, according to their mode of development, be arranged in the following groups :—

I. **Parietal muscles**, derived from the mesoblastic somites.

> *a. Muscles of the trunk,* including the coracohyoid (sterno-hyoid) of Fishes and its representatives in higher Vertebrates: these represent the oldest and most primitive part of the muscular system.
> *b. Muscles of the diaphragm.*
> *c. Muscles of the extremities.*
> *d. Eye-muscles.*

II. **Visceral muscles**, derived from the lateral plates of the mesoblast.

> *Cranial muscles,* with the exception of those included under *a* and *d* above.

In its simplest form, an *origin*, a *belly*, and an *insertion*, may be distinguished in each muscle. The muscles of the trunk are as a

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[1] Exceptions are seen in the muscles of the heart, and of the alimentary canal in the Tench. More or less of the anterior and posterior parts of the digestive canal may contain striated fibres in other animals.

rule flat, while those of the extremities have usually an elongated, cylindrical, or prismatic form. In some cases, however, they assume the most various shapes: for instance, there may be more than one origin (bicipital, tricipital, or quadricipital forms), the belly may be double (biventral or digastric form), or the muscle may be saw-shaped, or have its fibres arranged in a single or double series like a feather.

All the muscles are surrounded by fibrous sheaths, or *fasciæ*, by means of which they are more or less firmly connected with one another and with the integument and skeleton. Wherever a marked friction occurs, ossifications (*sesamoids*) may become developed in the course of a muscle or tendon.

The differentiation of independent muscles may take place—(1) by the separation of the originally single muscle into proximal and distal parts by the formation of an intermediate tendon ; (2) by the splitting of a muscular mass into layers ; (3) by a longitudinal splitting ; or (4) by a fusion of distinct muscles. A muscle may undergo very considerable modification both in form and position by a change of origin and insertion ; and when the action of a muscle becomes unnecessary, it either disappears partly or entirely, or what remains of it contributes to the strengthening of a neighbouring muscle.

The following important factors must be taken into consideration in connection with the muscular system : (1) the homologies of the parts of the skeleton; (2) the relative positions of the neighbouring soft parts; and (3) the nerve-supply.

Most of the muscles bear a close relation to the skeleton from which they take their origin and into which they are inserted. The **integumentary musculature**, on the other hand, lies entirely in the subcutaneous connective tissue, but in Mammals its origin can be traced to the deeper, skeletal muscles: this is most plainly seen in Monotremes. Only slightly developed in the Anamnia, it becomes of great importance in Reptiles and Birds on account of its relations to the scutes, scales, and feathers. It is most highly developed amongst Mammals, where it may extend over the back, head, neck, and flanks as the *panniculus carnosus* (Echidna, Dasypus, Pinnipedia, Erinaceus, &c.). In Man, only a rudiment of this muscle is found in the shape of the *platysma myoides*, which extends over the neck and part of the breast and face.

The action of the integumentary muscles is very different in different Vertebrates. It may (1) serve to roll the body up into a ball (*e.g.*, Hedgehog, Armadillo) ; (2) be connected with a tail adapted for swimming (*e.g.*, Ornithorhynchus) ; (3) serve to erect the integumentary spines (*e.g.*, Echidna) ; or (4) cause local movements ("twitching") of the skin (many Mammals).

The *facial muscles*, though present in rudiment in the Anamnia, form a marked feature for the first time in Mammals, arising mainly in connection with the platysma myoides, and gradually extending

over the face so as to become grouped around the eyes, nose, mouth, and ears. They are supplied by the facial nerve, and attain their greatest development in the Primates, in which certain other facial muscles are derived from the deeper-lying *sphincter colli*.

## Parietal Muscles.

### A. *Muscles of the Trunk*.

In **Amphioxus** (Fig. 219) the body muscles are made up of a series (60 or more) of lateral muscular segments or *myotomes* separated by > shaped connective-tissue septa or *myocommata*, between which the fibres run longitudinally. The myotomes have an alternating arrangement on the two sides. On the ventral region of the anterior two-thirds of the body there is a thin transverse sheet of fibres.

In **Fishes** and **Dipnoans** the myotomes and myocommata are arranged in pairs and consist, on either side of the body, of two portions, a dorsal and a ventral, separated from one another by a connective-tissue septum extending from the axial skeleton to the integument (comp. Fig. 116).[1] The myotomes meet together in the mid-dorsal and mid-ventral lines.

This primitive metameric arrangement of the lateral muscles of the trunk forms a characteristic feature in Vertebrates, and stands in close relation with the segmentation of the axial skeleton and spinal nerves, the number of vertebræ and pairs of nerves corresponding primitively to that of the myotomes.

The lateral muscles largely retain their primitive relations in Fishes and Dipnoans, but on the ventral side of the trunk, where they enclose the body-cavity (comp. Amphioxus), certain differentiations occur which indicate the formation of the recti and obliqui abdominis of higher types. The dorsal portions of these parietal muscles, as well as the ventral portions in the caudal region, retain the more primitive relations.

**Amphibia.**—In Urodeles (Figs. 116 and 117) *primary* and *secondary* ventral trunk-muscles can be distinguished, and both of these groups, like the dorsal muscles, are segmented. The former group consists of internal and external *obliqui* and *recti*. The secondary muscles arise by delamination from the primary, and give rise to a superficial *external oblique*, a superficial *rectus*, a *transversalis*, and a *subvertebralis*. These, however, only attain importance in caducibranchiate forms, in which they become marked during metamorphosis, and the primary musculature then

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[1] This septum is not present in Myxinoids, and is absent in Petromyzon and Lepidosteus posteriorly to the gills.

undergoes more or less reduction. Thus various conditions of the ventral musculature are found amongst Urodeles.

In the Anura, on the other hand, both primary and secondary muscles present a marked uniformity and relative simplicity; in the adult they give rise to a segmented rectus, an obliquus externus, and a transversalis, as well as to a cutancus abdominis derived from the external oblique. No trace of an internal oblique can be seen in the adult.

**Reptiles.**—In Reptiles, the lateral muscles of the trunk attain a much higher grade of development. This is to be accounted
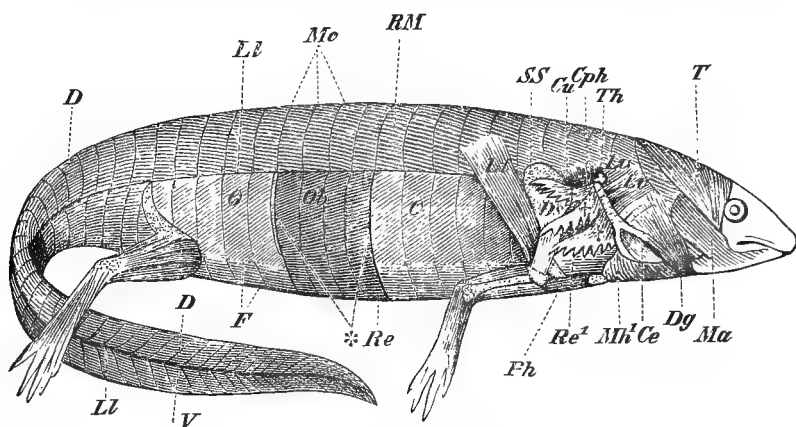


Fig. 116.—The Musculature of *Siredon pisciformis.* (From the side.)

*Ll*, lateral line; *D*, dorsal, and *V*, ventral portion of caudal muscles; *RM*, dorsal portion of lateral muscles of the trunk; *O, O*, outer layer of the external oblique muscle, arising from the lateral line, and extending to the fascia, *F*; at * a piece of this layer is removed, exposing the inner layer of the muscle (*Ob*); at *Re* the oblique fibres of the latter pass into longitudinal fibres, indicating the beginning of the differentiation of a rectus abdominis; at *Re*[1] the rectus-system is seen passing to the visceral skeleton; *Mc*, fibrous partitions between the myotomes of the dorsal portion of the lateral muscles; *T*, temporal; *Ma*, masseter; *Dg*, digastric; *Mh*[1], mylohyoid (posterior portion); *Ce*, external ceratohyoid muscle; *Lr*, levator arcuum branchialium; +++, levator branchiarum; *Cph*, cervical origin of the constrictor of the pharynx; *Th*, thymus; *Lt*, latissimus dorsi; *Ds*, dorsalis scapulæ; *Cu*, cucullaris; *SS*, suprascapula; *Ph*, procoraco-humeralis.

for by the more perfect condition of the skeleton, more especially of the ribs and pectoral arch. The ribs and intercostal muscles now play an important part in respiration, and changes, necessitated by the more important development of the lungs, are thus brought about.

The distinction between thoracic and abdominal regions becomes gradually more plainly marked, and distinct *external* and *internal intercostal muscles* are now differentiated. In the lumbar region the ribs become gradually withdrawn from the muscles lying

between them; the muscles thus lose their intercostal character, and form connected sheets, extending between the last pair of ribs
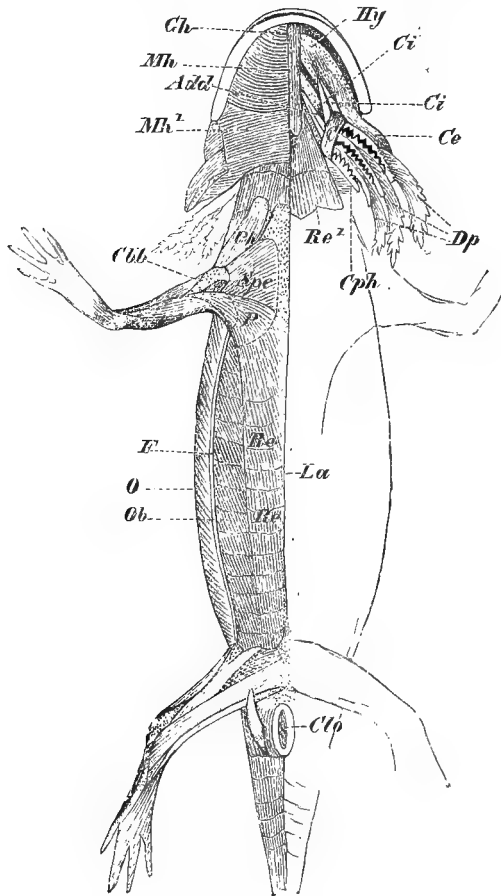


FIG. 117.—THE MUSCULATURE OF *Siredon pisciformis.*   (Ventral view.)

*O*, outer layer of the external oblique, passing into the fascia, which is shown cut through at *F*; *Ob*, inner layer of the same muscle; *Re*, rectus abdominis, passing into the visceral musculature (sternohyoid) at *Re*[1], and into the pectoralis major at *P*; *Mh*, *Mh*[1], anterior and posterior portions of the mylohyoid, which is cut through in the middle line, and removed on the left side, so as to show the proper visceral musculature; *Ce*, *Ci*, *Ci*[1], external and internal ceratohyoid: the former is inserted on to the hyoid (*Hy*); *Add*, adductor arcuum branchialium; *C*, constrictor arcuum branchialium; *Cph*, portion of the constrictor of the pharynx, arising from the posterior branchial arch; *Dp*, depressores branchiarum; *Gh*, genio-hyoid; *Ph*, procoraco-humeralis; *Spc*, supracoracoideus; *Cbb*, coraco-branchialis brevis; *Clo*, cloaca; *La*, linea alba.

and the pelvic arch (*e.g.*, the *quadratus lumborum*, which lies close against the vertebral column).

The rectus abdominis, which is always well developed, but does not extend anteriorly to the sternum, becomes divided into three portions,—a ventral, an internal, and a lateral.

While no important differentiation is noticeable in the dorsal portion of the lateral body-muscles in Urodeles, a marked subdivision of these muscles is seen in Reptiles.   In them may be distinguished a *longissimus*, an *ilecostalis*, *interspinales*, *semispinales*, *multifidi*, *splenii*, and *levatores costarum*, together with the *scaleni*, certain of which belong to the last-mentioned group, and others to the intercostal muscles.

The muscles of the main part of the tail retain primitive relations similar to those seen in Fishes : at the root of the tail and in the cloacal region, however, new muscles become differentiated.

**Birds.**—In Birds the primitive character of the trunk-muscles has disappeared far more than in Reptiles.   This is mainly to be accounted for by the excessive  development of the muscles of the anterior extremity—the *pectoralis major* more particularly,—and the corresponding backward extension of the breastbone.

External and internal oblique muscles are present, but only slightly developed : this is more particularly true of the internal, which appears to be undergoing degeneration.   No trace of a transversalis can be distinguished ; but, on the other hand, a paired, unsegmented rectus is present.

External and internal intercostals are well developed, and a *triangularis sterni* appears for the first time on the inner surface of the sternal ends of the ribs.

The dorsal portion of the trunk musculature is only slightly developed in the region of the trunk, though very strongly marked in the neck.

All these modifications in Birds seem to be accounted for by the specialisation of the mechanisms for flight and respiration, to assist which the greatest possible number of muscles are brought into play and thereby influence the whole organism : an essential difference is thus brought about between Birds and Reptiles.

**Mammals.**—Three lateral abdominal muscles are always present in Mammals, an external and internal oblique and a transversalis.  In many cases, more particularly in Tupaia and in Lemurs, the external oblique possesses tedinous intersections, thus indicating its primitive segmental character ; but in general all these muscles consist of broad uniform sheets.   Towards the middle line they pass into strong aponeuroses, which ensheath the rectus abdominis.   The latter consists of a single band on each side and possesses a varying number of myocommata ; it is no longer connected with the axial muscles of the neck belonging to the same system (sternohyoid, sternothyroid, &c.) as is the case in Urodeles,

for the sternum is always interposed between them, as it is in the Sauropsida.

In Monotremes and Marsupials, a strong *pyramidalis* muscle lies on the ventral side of the rectus abdominis. It arises from the inner border of the "marsupial bones" (epipubes, p. 121) and may extend forwards as far as the sternum. In the higher Mammals, where the epipubes are absent, the pyramidalis usually becomes greatly reduced or entirely lost. Traces of it are, however, commonly to be met with even in the Primates, and always arise from the anterior border of the pubis, right and left of the middle line.

The external and internal oblique muscles are represented in the thoracic region in Mammals, as in the Sauropsida, in the form of external and internal intercostals.

What has been said above as to the differentiation of the dorsal portion of the trunk-muscles in Reptiles applies also essentially to Mammals.

The greater number of the muscles in connection with the external genital organs become differentiated from the primitive *sphincter cloacæ :* the origin of the others is not known.

B. *Muscles of the Diaphragm.*

A complete *diaphragm* dividing the cœlome into thoracic and abdominal cavities occurs only in the Mammalia. It is dome-shaped and muscular, its muscles arising from the vertebral column, ribs, and sternum. The diaphragm is of great importance in respiration, as it allows of a lengthening of the thoracic cavity in a longitudinal direction. It is supplied by a phrenic nerve, arising from one or more (3rd to 6th) of the cervical nerves ; and usually consists of a central tendon, perforated by the œsophagus and post-caval vein, and of muscular fibres radiating from this to the periphery and forming dorsally two strong "pillars of the dia-phragm." In some cases (*e.g.,* Echidna, Phocæna) the diaphragm is entirely muscular.

Amongst the Sauropsida, a partition is present between the pleural and peritoneal cavities in Chelonians, and is still more marked in Crocodiles and Birds[1]: this is connected with the ribs by muscular fibres. It, however, does not enclose the peri-cardium, which, as in the Anamnia, lies in the general peritoneal cavity.

The evolution of the mammalian diaphragm is not yet tho-roughly understood.

[1] In Birds, two entirely different structures have been described as a diaphragm. (*See* under *Air-sacs.*)

C. *Muscles of the Appendages.*

The most primitive condition of the muscles of the extremities is met with in Fishes and Dipnoans, in which the musculature of each surface of the fin forms a more or less uniform mass which may become differentiated into layers. Everything goes to prove that all the muscles of the appendages are to be looked upon primarily as derivatives of the lateral muscles of the trunk, *i.e.,* of the myotomes; and although in the Amniota they have apparently an independent origin, this is probably only due to an abbreviation of development.

Two principal groups of appendicular muscles may always be distinguished : one lying in the region of the pectoral and pelvic arches, dorsally and ventrally, the other in the free extremity. In Fishes and Dipnoans the latter consist essentially of elevators, adductors, and depressors of the fins ; while from the Amphibia onwards, in correspondence with the more highly-differentiated organs of locomotion, considerable complication is seen, and there is a much more marked separation into individual muscles corresponding with the different sections of the extremity. Thus *elevators*, *depressors*, *rotators*, *flexors*, *extensors*, and *adductors* are present in connection with the upper arm and thigh, fore-arm and shank, and hand and foot, and the digits are also moved by a highly-differentiated musculature. The number of muscles gradually increases in passing from the Urodela through the Sauropsida to the Mammalia.

When, as in the Primates, the anterior extremity is converted into a prehensile organ, new groups of muscles appear known as *pronators* and *supinators*. The former are derived from flexors, the latter from extensors.

D. *The Eye-Muscles.*

(These will be treated of in connection with the organ of vision.)

## Visceral Muscles.

**Fishes.**—Considerable differences exist in the visceral musculature of Fishes.[1] In Elasmobranchs, Fürbringer classifies these muscles as follows :—

  *A. Cranial muscles* (consisting originally of transverse or circular fibres) supplied by the $V^{th}$, $VII^{th}$, $IX^{th}$, and $X^{th}$ cerebral nerves.

[1] In *Cyclostomes* there is a remarkable transformation of the cranio-visceral musculature in correspondence with their peculiar cranial skeleton (suctorial apparatus) and branchial basket.

1. Constrictor arcuum visceralium, incl. constrictor superficialis dorsalis and ventralis.

*Innervation.*

| | |
|---|---|
| Levator labii superioris<br>  ,,     maxillæ  ,,<br>  ,,     palpebræ nictitantis [1] | V. |
|   ,,     rostri<br>  ,,     hyomandibularis<br>Depressor rostri<br>  ,,     mandibularis and hyomandibularis | VII. |
| Interbranchiales . | IX, X. |
| Trapezius | X. |

2. Arcuales dorsales .             IX, X.
3. Adductores, incl. adductor mandibulæ     V.
      and adductores arcuum branchialium.    IX, X.

B. *Spinal muscles* (originally longitudinal), divided, like the trunk-muscles, into myotomes. Supplied by the spino-occipital ( = the " ventral roots " of X) and spinal nerves.

(*a*) Epibranchial spinal muscles, dorsal to visceral skeleton.

*Innervation.*

4. Subspinalis .           .•    Spino-occipital nerves.
5. Interbasales.          . $\left\{\begin{array}{l}\text{Spino-occipital nerves,}\\\text{as well as the first}\\\text{spinal nerve.}\end{array}\right.$

(*b*) Hypobranchial spinal muscles, ventral to visceral skeleton.

6. Coraco-arcuales, incl. coraco-branchiales, coraco-hyoideus, and coraco-mandibularis .     $\left\{\begin{array}{l}\text{Spinal nerves, and}\\\text{partly the last one or}\\\text{more of the spino-}\\\text{occipital nerves.}\end{array}\right.$

The structure of the cranio-visceral musculature of Ganoids and Teleosts differs considerably from that roughly sketched out above, so that the different groups of muscles must be arranged in an entirely different manner. Thus in Teleostei the following divisions may be distinguished :—(1) Muscles of the jaw, (2) muscles of the dorsal, and (3) muscles of the ventral ends of the visceral arches. Each of these groups may again be sub-divided, but further details about their arrangement, which is often very complicated, cannot be given here. The visceral muscles of Polypterus are of especial interest, as they show an intermediate condition between those of Elasmobranchs and Urodeles.

**Amphibia.**—It is to be expected, *à priori*, that the musculature of the visceral skeleton should be more highly developed in branchiate than in air-breathing Amphibians ; we thus find that in the former more primitive relations are met with, connect-

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[1] This muscle has therefore nothing to do with the other eye-muscles.

ing them with lower forms, while in the latter a greater modification, or rather reduction, of these muscles takes place.

Between the two rami of the lower jaw is situated a muscle with transverse fibres (the *mylohyoid*), supplied by the third division of the trigeminal and the facial nerve ; this represents the last remnants of the constrictor muscle of Fishes. As the elevator of the floor of the mouth, it stands in important relation to respiration and deglutition, and is retained throughout the rest of the Vertebrata up to Man (Figs. 116, 117).

A continuation of the trunk-musculature (the *omo-*, *sterno-*, and *genio-hyoid*) provided with tendinous intersections, lies above the mylohyoid (Fig. 117). These muscles, which serve to pull the visceral skeleton forwards and backwards, are supplied by the first and second spinal nerves.

In contrast to Fishes, there is in Amphibians a definite differentiation into muscles of the tongue, that is, into a *hyoglossus* and a *genioglossus ;* but these also must be considered as having been derived from the anterior end of the ventral muscles of the trunk ; they are present in all Vertebrates, from the Amphibia onwards, and are supplied by the hypoglossal (= the first spinal nerve of Amphibians).

In the Perennibranchiata and in Salamander larvæ the muscles of the hyoid and of the visceral arches may, as in Fishes, be divided into a ventral and a dorsal group ; the latter disappears in adult Salamanders and Anurans, only the ventral persisting. Their function is to raise and depress the branchial arches, as well as to draw them forwards and backwards. To these may be added constrictors of the pharynx, as well as (in branchiate forms) levators, depressors, and adductors of the external gill filaments (Figs. 116 and 117). They are innervated by the vagus and glossopharyngeal.

The jaw-muscles include a depressor (*digastric*, or *biventer mandibulæ*, Fig. 116), supplied by the facial nerve, and elevators of the lower jaw (*masseter*, *temporal*, and *pterygoid* muscles), supplied by the third division of the trigeminal. All these muscles, which may be derived from the adductor of the mandible of Elasmobranchs and Ganoids, arise from the auditory region of the skull.

**Amniota.**—With the simplification of the visceral skeleton in Amniota there is a considerable reduction of the musculature belonging to it. All muscles connected with branchial respiration are of course wanting, and the ventral trunk-muscles, as mentioned above, are always interrupted in their forward extension by the sternum and pectoral arch. At the same time, the muscles along the neck and on the floor of the mouth met with in Amphibia are present here also ; they are, a mylo-, sterno-, omo-, and genio-hyoid, as well as a hyoglossus and genioglossus. To these may

be also added a sterno-thyroid, from which a thyro-hyoid is continued forwards.

. The stylo-hyoid, stylo-glossus, and stylo-pharyngeus of Mammals, arising from the styloid process and stylo-hyoid ligament and undergoing numerous variations, are peculiar to Mammals. They are supplied partly by the facial nerve, partly by the glossopharyngeal, and act as retractors of the tongue and levators of the pharynx and hyoid.

The muscles of the jaws resemble those of Amphibia, although, especially in the case of the pterygoids,[1] they are much more sharply differentiated, and are throughout more strongly developed.

[1] For the tensor tympani and stapedius muscules, *see* under Auditory Organ.

# D. ELECTRIC ORGANS.

ELECTRIC organs are present in certain Fishes, being most strongly developed in certain Rays (Torpedinidæ, *e.g.*, *Torpedo*, *Hypnos*) found in the Atlantic Ocean and various southern seas, in a South American Eel (*Gymnotus electricus*) and in an African Siluroid (*Malopterurus electricus*). Gymnotus possesses by far the strongest electric power, next to it comes Malopterurus, and then Torpedo. The electric batteries of these three Fishes are situated in different parts of the body : in the Torpedinidæ they have the form of a broad mass, extending throughout the substance of the part of the body lying between the gill-sacs and the propterygium on either side of the head (Fig. 118); in Gymnotus they lie in the ventral region of the enormously long tail (Fig. 119), that is, in the position usually occupied by the ventral portions of the great lateral muscles; and finally, in Malopterurus, the electric organ extends between the skin and muscles round almost the entire circumference of the body, thus enclosing the Fish like a mantle : it is especially strongly developed along the sides.



FIG. 118. — *Torpedo marmorata*, WITH THE ELECTRIC ORGANS (*E*) EXPOSED.

*S*, skull ; *Sp*, spiracle ; *KK*, gills ; *Au*, eye.

The electric power of those Fishes which were formerly known as " pseudo-electric " has now been fully demonstrated, though it is much feebler than in the forms described above. To this category belong all the Rays, excluding the Torpedinidæ, the various species of *Mormyrus*, and *Gymnarchus* (both the latter genera belonging to the Teleostei). In all these, the electric organs lie on either side of the end of the tail and have a metameric arrangement like that of the caudal muscles ; in the

Mormyridæ, for example, there is on each side an upper and lower row of electric organs.

The electric apparatus in all the above-named Fishes is to be regarded from the same point of view both as concerns its mode of development and its anatomical relations : *all electric organs are to be looked upon as consisting of metamorphosed muscular fibres and the nerve-endings belonging to them as homologues of the motor end-plates which are ordinarily found on muscles.*

As regards the structure of the electric organs, the same essential arrangements are met with in all : the details of their histology and physiology cannot be entered into here. The framework is formed of fibrous tissue enclosing numerous cells, which, running partly longitudinally, partly transversely through the organ, gives rise to numerous polygonal or more or less rounded chambers or compartments. These latter are arranged in rows, either along the longitudinal axis of the body (Gymnotus, Malopterurus) or in a dorso-ventral direction



FIG. 119, A and B.—THE ELECTRIC ORGAN OF *Gymnotus electricus.* (B, from a preparation by A. Ecker.)

*H*, skin ; *Fl*, fin ; *DM, DM¹*, dorsal portions of the great lateral muscles, seen partly in transverse, partly in longitudinal, section ; *VM, VM¹*, ventral portions of ditto ; *E*, the electric organ, seen in transverse section at *E* (B), and from the side at *E¹* ; *WS*, vertebral column from the side, and the spinal nerves, and *WS¹*, in transverse section ; *LH*, posterior end of body cavity ; *Sep*, median longitudinal fibrous septum between the left and right electric organ and lateral trunk-muscles ; *A*, anus.

(Torpedo), forming definite prismatic columns (Fig. 120).

Numerous vessels and nerves ramify in the connective-tissue lying between these compartments, the nerves being enclosed in thick sheaths, and having a different origin in the different forms. In Torpedo, in which the electric organs probably arise in connection with the great adductor muscle of the mandible

and the constrictor of the gill-arches, the nerves arise from the "electric lobe" of the medulla oblongata, a single branch coming also from the trigeminal nerve; in all pseudo-electric Fishes, as well as in Gymnotus, in which over two hundred nerves pass to the electric organ, they arise from the spinal cord, and are probably in close relation with the ventral cornua of the latter, which are particularly well developed in the last-named Fish. It is remarkable that the electric nerves of Malopterurus arise on each side from a single enormous lens-shaped nerve-cell, which, lying in the neighbourhood of the second spinal nerve, is continued into a very large primitive-fibre which passes towards the end of the tail, dividing as it goes. This fibre is invested by a thick sheath.
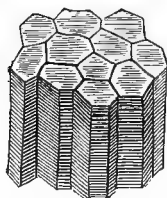
FIG. 120.—ELEC-
TRIC PRISMS OF
*Torpedo mar-
morata.* (Semi-
diagrammatic.)

Experiments have shown that all Electric Fishes are proof against the electric current, with the limitation that muscles and nerves—even the electric nerves themselves—separated out from the body are capable of being excited by the current. "The last and most important question with regard to the Electric Fishes is naturally concerning the mechanism whereby the electric plates become temporarily charged with electricity. The reply to this question, although probably not so difficult a one as that relating to the mechanism of muscular contraction, is still far from being answered" (Du Bois-Reymond). The only thing that can be stated with certainty is, that the electromotive force is under the influence of the will.

## E. NERVOUS SYSTEM.

THE nervous system, as already mentioned in the Introduction (p. 5), arises from the epiblast, and the first parts to become differentiated histologically are the **nerve-cells** (*ganglion-cells*), from which **nerve-fibres** arise later and serve as conductors of nervous impulses. The most important constituent of the nerve-fibre is a central *axis-cylinder* or *axis-fibre*, and in those nerve-fibres which are spoken of as medullated this is surrounded by a highly refractile, fat-like substance (myelin), which forms the *medullary sheath*. In certain (non-medullated) nerve-fibres this sheath is wanting, but the two kinds of fibres are not sharply marked off from one another, either locally or genetically: a fibre may be medullated in one part of its course, and non-medullated in another. Externally each nerve-fibre is enclosed by a delicate sheath, the *neurilemma*.

Part of the epiblastic tissue which forms the nervous system of the embryo does not become transformed into nervous tissue, but gives rise to a supporting and connecting framework—the *neuroglia*; and externally, investing membranes as well as blood and lymph-vessels, are formed from the mesoblast.

The nervous system consists of *central* and *peripheral* portions (Fig. 121). The central part (*brain* and *spinal cord*) is the first to arise, and is formed as a direct product of the epiblast; the peripheral portion (*cerebral, spinal*, and *sympathetic nerves*) becomes established later.

## 1. THE CENTRAL NERVOUS SYSTEM.

The first indication of the central nervous system is a longitudinal furrow (*medullary groove*, Fig. 6, A) which appears on the dorsal side of the embryo and gradually becomes converted into a tube by the meeting of its edges; this tube, consisting originally of epithelial cells like the epiblast from which it arises, then becomes separated from the epiblast and gives rise to the hollow *medullary cord*[1] (Fig. 6, B), in which nerve-cells and fibres soon become differentiated; it comprises a more expanded anterior and a longer and more slender posterior section. From the former arises the **brain,** from the latter the **spinal cord.**

[1] The cord is at first solid in Cyclostomes, Teleosts, and bony Ganoids, cavity being formed secondarily.
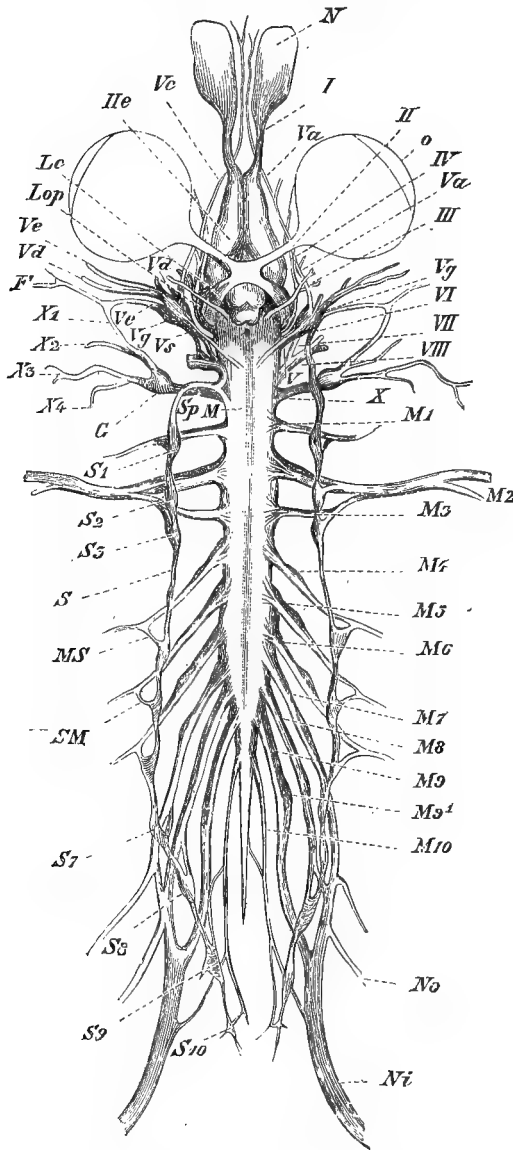
Fig. 121.—The Entire Nervous System of the Frog. (After A. Ecker.)
From the ventral side.

*He*, cerebral hemispheres (prosencephalon) ; *Lop*, optic lobes (mesencephalon),
*M*, spinal cord ; *M1* to *M10*, spinal nerves, which are connected at *SM* by
branches (rami communicantes) with the ganglia (*S1* to *S10*) of the sympathetic
(*S*) ; *No*, femoral nerve ; *Ni*, sciatic nerve ; *I* to *X*, first to tenth cranial
nerves ; *G*, ganglia of the vagus ; *Vg*, Gasserian ganglion ; *o*, eye ; *N*, nasal
sac ; *Va* to *Ve*, the different branches of the trigeminal ; *F*, facial nerve ;
*Vs*, connection of the sympathetic with the Gasserian ganglion ; *X1* to *X4*,
the different branches of the vagus. Some of the fibres of the sympathetic
should be shown accompanying the vagus peripherally.

In an early stage of development the lumen of the medullary cord is primitively continuous posteriorly with that of the primary intestine (*neurenteric canal*). This connection, however, soon disappears, and the cord then consists of a cylindrical or more or less flattened hollow cord with thick walls, the cavity of which is lined by ciliated epithelium and expands in front to form the *ventricles* of the brain. This cavity becomes greatly reduced later, and in the spinal cord is spoken of as the *central canal*.

### Membranes of the Brain and Spinal Cord.

The enveloping membranes of the brain and spinal cord arise by the differentiation of a connective-tissue layer lying between the central organs of the nervous system and the surrounding skeletal parts. In Fishes, only two membranes are distinguishable :—one,
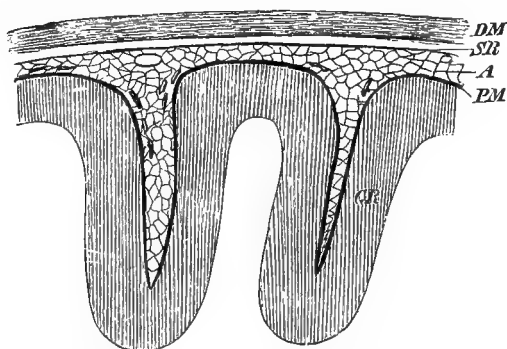


FIG. 122.—BRAIN MEMBRANES OF MAN.    (After Schwalbe.)

*DM*, dura mater ; *SR*, sub-dural (arachnoid) space ; *A*, sub-arachnoid space ; *PM*, pia mater ; *GR*, gray cortical substance of the brain.

the *dura mater*, lining the inner surface of the cerebro-spinal canal, and the other, or *pia mater*, investing the brain and spinal cord. The latter represents also the *arachnoid* of higher Vertebrates, which is not here differentiated as a separate membrane. The dura mater conveys vessels to the walls of the cerebro-spinal canal—that is, to the perichondrium or periosteum, while the pia mater, which is much richer in blood-vessels, has to do with the nutrition of the nervous axis. The dura mater consists of two lamellæ, which, however, only remain distinct along the whole central nervous system in the lower Vertebrata. In higher Vertebrates, its double nature persists only in the region of the vertebral column, the two layers becoming fused in the cranial portion. As in most Fishes the brain by no means fills the cranial cavity, a large lymph-space lies between the dura and pia mater; this corresponds to the so-called sub-dural space of terrestrial Vertebrates.

A differentiation of the primary vascular membrane of the brain and spinal cord into pia mater and arachnoid takes place from the Amphibia onwards, and these two layers become separated in those places where there are deep depressions between the individual parts of the brain; the deeper of these (pia) adheres closely to the brain, and also penetrates into the ventricles in the form of *telæ choroideæ* and *plexus choroidei*, while the superficial one (arachnoid) simply bridges over the depressions (Fig. 122). A lymph-sinus (sub-arachnoid space) is thus developed between the two in the Sauropsida and Mammalia, but this never reaches such an independent differentiation as does the sub-dural (arachnoid) space.

## 1. The Spinal Cord.

The spinal cord is at first of a uniform diameter throughout, but as a richer nerve-supply becomes needed for the extremities, it exhibits in these regions definite swellings — the *brachial* and *lumbo-sacral* enlargements (Fig. 123). The cord originally extends along the whole length of the neural canal, but its growth is usually less rapid than that of the vertebral axis, so that eventually it is considerably shorter than the latter. In such cases (*e.g.* Primates, Cheiroptera, Insectivora, Anura, Figs. 121 and 123) it passes at its posterior end into a brush-like mass of lumbo-sacral nerves, the so-called *cauda equina*, lying within the neural canal. A prolongation of the spinal cord nevertheless extends far back amongst these as a thin thread-like appendage, the *filum terminale*.

The bilaterally-symmetrical form of the spinal cord is pronounced by the presence of longitudinal *fissures* running along it dorsally and ventrally;[1] and if one imagines the points of exit of the dorsal and ventral nerve-roots to be respectively connected together by a longitudinal line, each half of the spinal cord would thus be divided into three columns,—a dorsal, lateral, and ventral.



FIG. 123.—DIAGRAMS OF THE SPINAL CORD AND ITS NERVES. In A the cord passes to the end of the tail, and at B it ends more anteriorly and passes behind into a filum terminale (*F.t*).

*M.o*, medulla oblongata; *Pc*, cervical nerves; *Pb*, brachial nerves; *P.th*, thoracic nerves; *Pl*, lumbo-sacral nerves; *Ce*, cauda equina.

[1] The ventral fissure is not always present, and the so-called dorsal fissure, which is formed by obliteration of the greater part of the primitive central canal, is better described as the dorsal *septum*.

As regards its minute structure, two parts can be distinguished in the spinal cord,—a *white substance,* consisting of nerve-fibres only, and a *gray substance,* composed of nerve-cells as well as fibres. Their relative positions vary in the different animal groups, as well as in the different regions of the cord ; the white substance, however, has typically a more peripheral, the gray a more central position, the latter surrounding the central canal and usually presenting a pair of *dorsal* and *ventral cornua* in transverse section.

## 2. The Brain.

Before the medullary groove becomes closed, the anterior expanded part of the medullary tube presents three swellings, which are spoken of as the primary *fore-, mid-,* and *hind-brain,* or *anterior, middle,* and *posterior cerebral-vesicles* (Fig. 124) ; the cavities of the vesicles (*ventricles*) are in direct connection with the central canal of the spinal cord. Both the primary fore-brain and hind-brain then become differentiated, each into two parts, and thus five



Fig. 124.—Diagram of the Embryonic Condition of the Central Nervous System.

*G,* brain, with its three primary vesicles, *I, II, III* ; *R,* spinal cord.

divisions of the brain may be distinguished. Counted from before backwards these are :—*prosencephalon* (secondary fore-brain), *thalamencephalon* (primary fore-brain), *mesencephalon* (mid-brain), *metencephalon* (secondary hind-brain), and *myelencephalon* (primary hind-brain). The prosencephalon usually gives rise to a pair of lobes, the *cerebral hemispheres,* and in the mid-brain a pair of *optic lobes* or *corpora bigemina* become differentiated dorsally, and two longitudinal bands, the *crura cerebri,* ventrally. The metencephalon is usually spoken of as the *cerebellum,* and the myelencephalon as the *medulla oblongata.*

From the base of the prosencephalon or hemispheres paired *olfactory lobes* (*rhinencephala*) are given off anteriorly, and the floor or central part of each hemisphere becomes thickened to form a large "basal ganglion," the *corpus striatum,* while its peripheral part is distinguished as the "mantle" or *pallium* (Fig. 125).

The relative development and differentiation of the pallium stands in close relation to the mental development of the animal, and reaches its greatest perfection in Mammals, especially in Man. In certain Fishes the pallium remains partially or entirely non-nervous, retaining its primitive epithelial character, and a layer

of cortical gray matter is only distinctly differentiated from Reptiles onwards. No regular series of gradations can, however, be traced in this respect in the various groups.

Connecting the two lateral halves of the fore-brain are certain transverse bands of nerve-fibres or *commissures*. An *anterior commissure* is present in the posterior region of the secondary fore-brain, a *middle* in the primary fore-brain, and a *posterior* in the anterior part of the mid-brain. In addition to these, others may be developed between the hemispheres, but only attain importance in Mammals : they are known as the *corpus callosum* and the *fornix*.

The outer surface of the hemispheres in all Vertebrates below the Mammalia is more or less smooth : in the latter Class, convolutions (*gyri*) separated by fissures (*sulci*) may be present. The
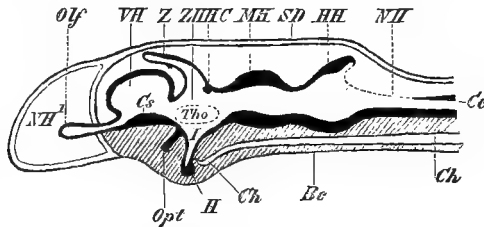


Fig. 125.—Diagrammatic Longitudinal Section through the Skull and Brain of an (Ideal) Vertebrate Embryo. (In part after Huxley.)

*Bc*, basis cranii ; *Ch*, notochord ; *SD*, roof of skull ; *NH¹*, nasal cavity ; *VH*, secondary fore-brain (prosencephalon), showing the corpus striatum (*Cs*) at the base, and the olfactory lobe (*Olf*) anteriorly ; *ZH*, thalamencephalon (primary fore-brain), which has given rise dorsally to the pineal body (epiphysis, *Z*), and ventrally to the infundibulum (*I*), to which the pituitary body (hypophysis, *H*) is attached : anterior to this is seen the optic nerve (*Opt*), arising from the optic thalamus (*Tho*) ; *HC*, posterior commissure ; *MH*, mid-brain (mesencephalon) ; *HH*, cerebellum (metencephalon, secondary hind-brain) ; *NH*, primary hind-brain (myelencephalon) ; *Cc*, central canal of spinal cord.

convolutions consist of folds of the gray cortical substance, which cause a greater or less increase of the superficial area.

From the *thalamencephalon,* the ventricle of which is walled-in anteriorly by the *lamina terminalis*, the following structures arise (Fig. 125) :—the *optic thalami,* formed as thickenings of its lateral walls ; the primary *optic vesicles,* arising as paired ventro-lateral outgrowths from which the *optic nerves* and *retina* are derived later ; the *pineal apparatus*, developed as tube-like outgrowths of the roof ; and finally, the *infundibulum,* formed as a funnel-like extension of the floor, together with a part of the *pituitary body* (*hypophysis*). The other portion of the pituitary body arises by a gradual pinching off of the epithelium of the primary oral involution (*stomodæum*, p. 5, and Fig. 126), which gives rise to a gland-like structure, and other parts (*saccus vasculosus*, &c.) arise in close connection with it.

The *pineal apparatus* consists of the *epiphysis* or *pineal organ proper*, which persists in a more or less rudimentary condition in all Vertebrates, and of a more anterior outgrowth which may be called the *parietal organ*, arising from the epiphysis or independently from the roof of the thalamencephalon ; the latter organ becomes atrophied in the majority of Vertebrates. Each of these structures represents a vestigial sensory organ, and in certain cases may retain to a greater or less extent the character of a *median eye*— possibly in some degree comparable to that of Tunicates.[1]

Certain facts seem to indicate that both organs arose primitively in a paired manner. Accessory vesicles occur occasionally in young Slow-worms (*Anguis*), in which as many as two or even three rudimentary vesicles may be present behind the pineal organ.
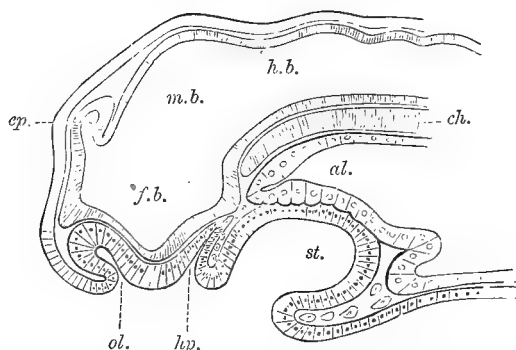


FIG. 126.—MEDIAN LONGITUDINAL SECTION THROUGH THE HEAD OF A NEWLY-HATCHED LARVA OF *Petromyzon planeri*. (Mainly after Kupfer.)

*f.b*, fore-brain ; *m.b*, mid-brain ; *h.b*, hind-brain ; *ep*, epiphysis ; *hp*, hypophysis ; *st*, stomodæum ; *al*, endodermic alimentary cavity ; *ch*, notochord.

The *hypophysis* apparently represents a glandular organ, the secretion of which formerly passed into the ventricles, and various hypotheses have been put forward as to its first origin.

One of the more recent of these theories assumes that it corresponds to the primitive mouth (*palæostoma*) of the Proto-Vertebrata, which is to a greater or less extent represented by the combined unpaired nasal and pituitary passage of Cyclostomes (see under Olfactory Organ) : the mouth of existing Vertebrates must then be distinguished as a *neostoma*.

Both the primary and the secondary fore-brain are situated in the pre-chordal region of the skull, all the other divisions of the brain lying in its chordal portion (comp. p. 67).

The mid-brain and medulla oblongata undergo fewer modifications than the fore-brain ; only the anterior part of the thin

[1] Still more anteriorly a third outgrowth or *paraphysis*, arising from the secondary fore-brain, has been observed in the embryos of various Vertebrates.

roof of the latter (*valve of Vieussens*) is nervous, and its floor becomes greatly thickened.    The greater number of the cerebral nerves arise from the medulla oblongata, so that its physiological importance is very great.    The cerebellum may become more or less distinctly subdivided into lobes.
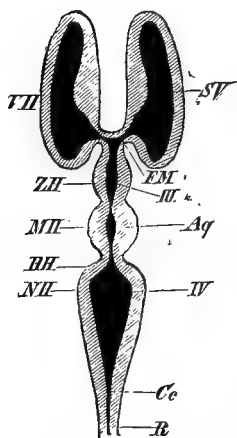


FIG. 127.—DIAGRAM OF THE VENTRICLES OF THE VERTEBRATE BRAIN.

*VH*, cerebral hemispheres containing the lateral (1st and 2nd) ventricles (*SV*) ; *ZH*, thalamencephalon, with the third ventricle (*III*) ; a thickened vascular part of the pia mater (*choroid plexus*) roofs over the third and fourth ventricles ; each lateral ventricle communicates with the third ventricle by a small aperture, the foramen of Monro (*FM*); *MH*, mid-brain, which encloses the aqueduct of Sylvius (*Aq*), communicating between the third and fourth ventricles ; *HH*, cerebellum ; *NH*, medulla oblongata, enclosing the fourth ventricle (*IV*) ; *Cc*, central canal of the spinal chord (*R*).

In the course of the development of the brain the walls of the cerebral vesicles become more and more thickened, so that their cavities undergo a gradual constriction.

A series of unpaired ventricles (*prosocœle, thalamocœle, mesocœle, metacœle, myelocœle,* see p. 153), lying in the longitudinal axis of the brain, as well as paired outgrowths from certain of them, can always be distinguished (Fig. 127).    When cerebral hemispheres are developed (as is generally the case), the prosocœle gives rise to paired cavities, extending into them, and known as the *lateral ventricles* (ventriculus 1 and 2); each of these communicates with the thalamocœle or *third ventricle* by means of an opening, the *foramen of Monro*, and may be continued into the corresponding olfactory lobe as a *rhinocœle* or *olfactory ventricle*.    Each optic lobe also usually contains an *optic ventricle*, or *optocœle*, communicating with the mesocœle or *aqueduct of Sylvius*.    There may be a distinct metacœle in the cerebellum opening into the myelocœle or *fourth ventricle*.

A so-called *fifth ventricle*, situated between the corpus callosum and fornix, is found in Mammals, but morphologically it has nothing to do with the ventricles proper, and simply represents a space between the thin internal walls (*septa lucida*) of the two hemispheres.

All five cerebral vesicles lie at first in the same horizontal plane, but in the course of development a *cerebral flexure* takes place, the axis of the vesicles becoming bent downwards, so that at a certain stage the mesencephalon forms the apparent apex of the brain.    In Mammals, the parts of the brain become still further folded on one another, so that a parietal, a Varolian, and a cervical bend may be distinguished (Fig. 128): this process is connected with the further development of the skull and the rapid longitudinal growth of the brain.

In Fishes and Amphibians the cerebral flexure later becomes practically obliterated, but it persists more or less markedly in the higher types, more particularly in Mammals. In the latter Class, moreover, the original relation of the parts becomes still further complicated by the large development of the cerebral hemispheres, which grow backwards, and thus gradually come to overlie all the other parts of the brain. This condition of things attains its greatest perfection in Man. Thus instead of the various sections of the brain being situated one *behind* another, they come to lie eventually more *upon* one another, the thalamencephalon, mid-brain, cerebellum, and medulla oblongata becoming covered over by the hemispheres.



FIG 128.—CEREBRAL FLEXURE OF A MAMMAL.

*VH*, prosencephalon; *ZH*, thalamencephalon, with the pituitary body (*H*) at its base; *MH*, mesencephalon, which at *SB* forms the most projecting portion of the brain, representing the so-called "parietal bend"; *HH*, metencephalon; *NH*, myelencephalon, forming the "cervical bend" (*NB*): the "Varolian bend" (*BB*) arises on the ventral circumference, at the junction between *HH* and *NH*; *R*, spinal cord.

**Amphioxus.**—The conical and enlarged anterior end of the spinal cord of the Lancelet contains a widened portion of the central canal which must be looked upon as a ventricle. In the larva, this opens freely on to the exterior dorsally by a *neuropore*, which probably represents the last indication of the primitive connection of the central nervous system with the outer skin. It is possible that the anterior enlargement of the cord corresponds to the fore-brain—and perhaps also the mid-brain—of the Craniata.

**Cyclostomi.**—The brain of these forms remains in many respects in an embryonic condition : this is particularly the case in the larval Petromyzon or Ammocœte (Fig. 129). In the adult the individual vesicles lie in an almost horizontal direction one behind the other, and the prosencephalon consists of a median part and of small paired hemispheres continuous anteriorly with the larger, rounded olfactory lobes. The median portion of the prosocœle is continued transversely outwards into each hemisphere, in which it gives rise to a lateral ventricle : this is continued forwards for a short distance into the base of the olfactory lobe, as well as backwards into the hemisphere. The roof (pallium) of the median portion of the ventricle is non-nervous, and consists of a *single layer of epithelial cells*, which, together with the pia mater, has been removed in the preparation represented in Fig. 129, A. The mid-brain and medulla oblongata are relatively broad, and the cerebellum is represented by a mere narrow ledge overhanging the fourth ventricle anteriorly. The roof of the mesocœle is formed mainly by a layer of epithelial cells, and, like that of the third and fourth ventricles, is

covered by a thickened and vascular portion of the pia mater. or
*choroid plexus.*
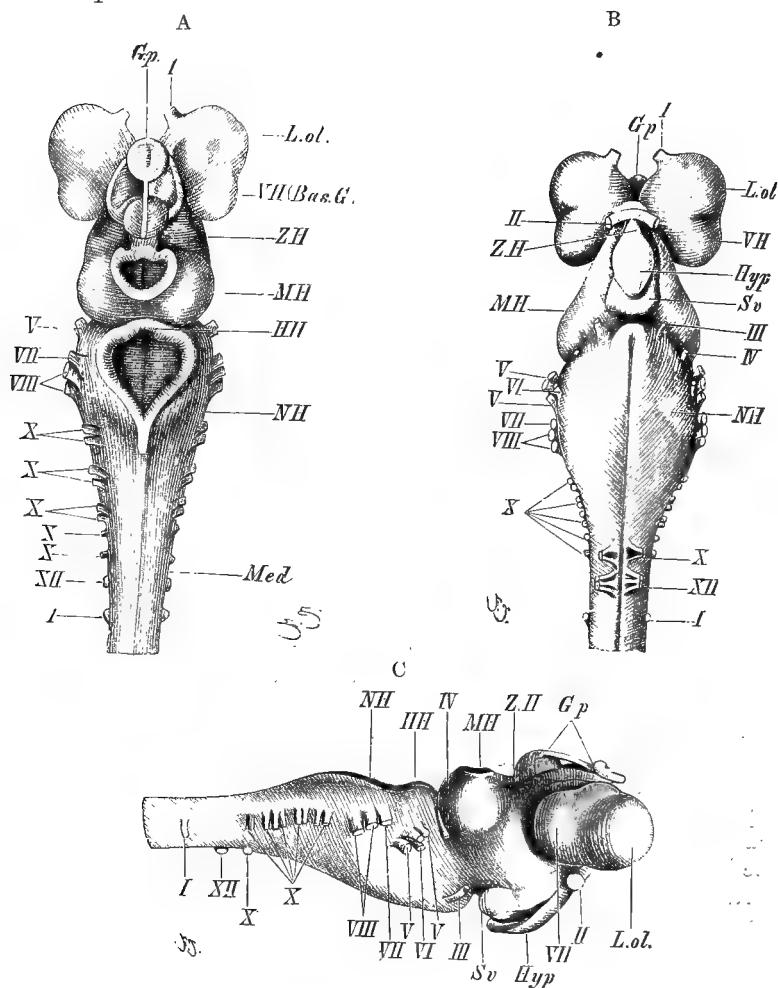


FIG. 129. —BRAIN OF LARVAL LAMPREY. (A, from above ; B, from below ;
C, from the side.)

*VH* (*Bas. G*), cerebral hemispheres, between which, in A, the median portion of the
prosencephalon is seen, with the membranous roof removed ; *L.ol*, olfactory
lobe ; *ZH*, thalamencephalon ; *G.p*, pineal body ; *Hyp*, hypophysis ; *Sv*,
saccus vasculosus ; *MH*, mid-brain ; *HH*, cerebellum ; *NH*, medulla oblon-
gata ; *Med*, spinal cord ; *I-X*, cranial nerves ; *XII*, first spinal nerve (hypo-
glossal).

The brain of Myxine shows many special peculiarities: its
subdivisions are broader and more closely approximated than in

the lamprey, and the thalamencephalon cannot be seen from the dorsal side owing to the larger size of the solid prosencephalon. The mesocœle ends blindly in front, the third ventricle being almost completely obliterated. The cerebellum is relatively larger than in Petromyzon, and no pallium has been recognised in the prosencephalon of the adult.

In Petromyzon the pineal apparatus is represented by two vesicles, each connected with the dorsal surface of the thalamencephalon (ganglion habenulæ) and lying one above the other just beneath the roof of the skull; the integument immediately above these vesicles is pigmentless. The cells on the ventral side of the dorsal vesicle (epiphysis) are arranged radially and contain pigment, forming a kind of retina, but they show signs of degeneration; the lower vesicle (parietal organ, p. 155) is without pigment. In Myxine there is only a single pigmentless vesicle.

A *saccus vasculosus* (comp. pp. 154, 160, *et seq.*) is present in connection with the infundibulum, to which a small pituitary body is attached.

**Elasmobranchii and Holocephali.**—The brain of these Fishes, like that of Cyclostomes, is in many respects of a specialised form, characteristic of, and confined to, the group, though the particular regions are much more highly developed than in the Cyclostomi. According to its external form two main types can be distinguished. One of these, seen in Spinax, Scymnus, Notidanus and the Holocephali, is characterised by its very narrow and elongated form, while in the rest of the Elasmobranchii the individual parts are more closely compressed and approximated together (Fig. 130). In almost all Sharks the prosencephalon is relatively much larger than any of the other regions. The olfactory lobes arise from the anterior or antero-lateral ends of the prosencephalon, and in some Elasmobranchs remain in close connection with the latter : in others in which the olfactory capsules are situated further forwards, they become drawn out into long *olfactory tracts* each continuous anteriorly with an *olfactory bulb* from which the olfactory nerves arise.

A division of the prosencephalon into paired halves is hardly indicated at all in Rays, and only slightly so in the commoner Dogfishes (*e.g.*, Scyllium, Acanthias), in which, however, lateral and olfactory ventricles are present. Only in Scymnus, and to some extent in the Notidanidæ, is there a distinct separation of the pallium into two hemispheres. In Rays there is only a small single prosocœle, the prosencephalon consisting of a practically solid mass, and the olfactory lobes are also solid.

The thalamencephalon is roofed over by a choroid plexus, and the tube-like epiphysis may reach such a length as to extend beyond the anterior end of the brain for a considerable distance, and pass distally into the roof of the skull : no indication can be seen of a parietal organ. A pair of small lobes—the *lobi inferiores*—are
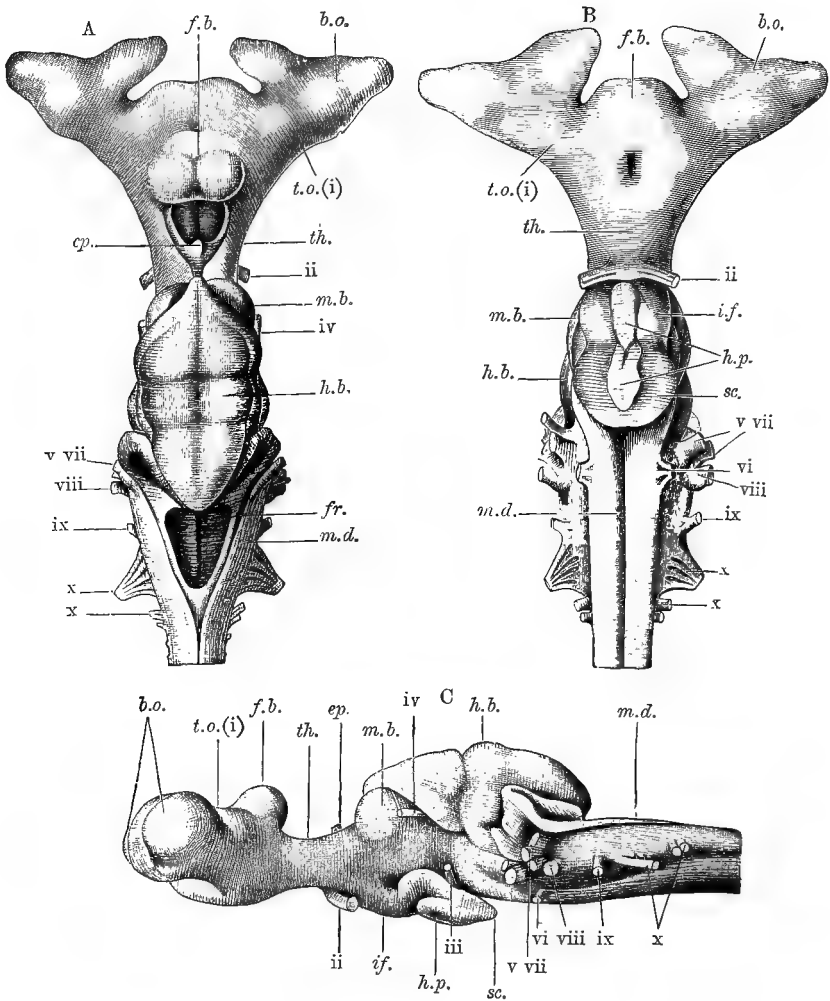
FIG. 130.—BRAIN OF *Scyllium canicula.* (A, dorsal ; B, ventral ; and C, lateral view.)

*f.b*, prosencephalon ; *b.o*, olfactory bulb ; *t.o*, olfactory tract (very short in *Scyllium*) ; *th*, thalamencephalon ; *ep*, base of pineal body ; *if*, lobi inferiores ; *h.p*, hypophysis ; *sc*, saccus vasculosus ; *m.b*, mid-brain (optic lobes) ; *h.b*, cerebellum ; *m.d*, medulla oblongata ; *fr*, fourth ventricle ; *i-x*, cranial nerves (the ventral vagus roots are omitted from Fig. B. The epithelial and vascular roof of the third and fourth ventricles has been removed.

present on the infundibulum, and an "infundibular gland" or saccus vasculosus is present on the sides and floor of the infundibulum, which is connected posteriorly with the pituitary body.

The cerebellum is always very large, overlapping the optic lobes and the medulla oblongata to a greater or less extent : it is divided up into several folds lying one behind the other, and usually contains a metacœle opening into the fourth ventricle (Figs. 130 and 131). In Sharks the medulla oblongata is an elongated cylindrical body, while in Rays it is more compressed and triangular ; at its
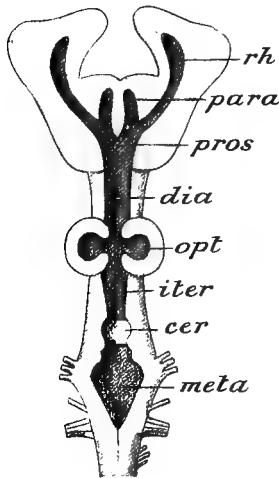


FIG. 131. — BRAIN OF *Cheiloscyllium*. (From Parker and Haswell's *Zoology*.)

Viewed from the dorsal side, the roof of the various ventricles removed so as to show the relations of the cavities (semi-diagrammatic).
*cer*, dilatation from which the metacœle is given off ; *dia*, thalamocœle—the reference line points to the opening leading into the infundibulum ; *iter*, aqueduct of Sylvius (mesocœle), into which the optocœles (*opt*) open ; *meta*, myelocœle ; *para*, lateral ventricle ; *pros*, median part of prosocœle ; *rh*, rhinocœle.
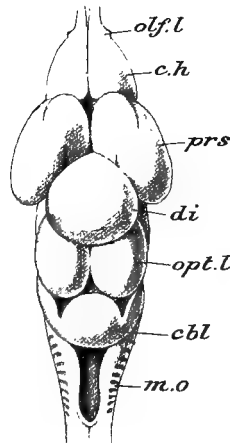


FIG. 132.—BRAIN OF *Lepidosteus*. (Dorsal view.) (After Balfour and Parker.)

*cbl*, cerebellum ; *c.h*, prosencephalon ; *di*, thalamencephalon ; *m.o*, medulla oblongata ; *olf.l*, olfactory lobes ; *opt.l*, optic lobes ; *prs*, lobes of prosencephalon.

anterior end are two lateral lobes, the *corpora restiformia*. In electric Rays (p. 146) a pair of *lobi electrici* arise from the gray matter of the floor of the fourth ventricle, and these enclose a mass of giant nerve-cells.

**Ganoidei.**—The pallium covering the median prosocœle consists mainly or entirely of *epithelial and connective tissue*

*elements*, much as in Cyclostomes. The olfactory lobes are closely applied to the prosencephalon, which gives rise anteriorly to cerebral hemispheres containing lateral ventricles (Fig. 132).

The well-developed thalamencephalon has a marked ventral flexure and from its roof arises a strong pineal peduncle, the distal end of which extends into a hollow in the cranial roof, but undergoes atrophy, in Amia becoming completely separated off from the brain.[1] Well-developed lobi inferiores are present, and the hypophysis[2] and saccus vasculosus are voluminous: the latter consists largely of glandular tubules which open into the infundibulum, as is also the case in Elasmobranchs (p. 160).

The large cerebellum gives rise to a *valvula cerebelli* (comp. Fig. 134) extending forwards into the ventricle of the mid-brain; the optic lobes are also large.

The brain of Amia on the whole most nearly approaches that of the Teleostei in structure.

**Teleostei.**—As is the case in many other Fishes, the brain in most Teleosts by no means fills the cranial cavity, and it is separated from the roof of the skull by a greater or less amount of a fatty and lymph-like fluid. It never attains to so large a relative size as does that of Elasmobranchs. Its form varies greatly, more by far than in any other Vertebrate group, and only the following essential points can be mentioned here.

The *pallium is entirely epithelial* in structure (Figs. 133–135), and, moreover, it presents no median involution dividing the anterior part of the prosencephalon into two lateral hemispheres: there is a median prosocœle. The lower part of the prosencephalon is made up of large paired basal ganglia (corpora striata) connected together by an anterior commissure. The olfactory lobes are either closely applied to the prosencephalon and contain a small rhinocœle, or they become differentiated into olfactory tract and bulb, as in Elasmobranchs (p. 159).

The thalamencephalon is very small. The epiphysis (Figs. 133, 134) is plainly distinguishable, but it does not pass into the roof of the skull; an outgrowth arising from the roof of the brain in front of the epiphysis represents the parietal organ, but this becomes constricted off from the brain and disappears during development.[3] Marked lobi inferiores, as well as a

[1] In Polypterus the pineal body gives rise to a peculiar and extremely large epithelial vesicle. In Devonian Ganoids there was a parietal foramen (comp. p. 171).

[2] In Polypterus and Calamoichthys the hypophysis communicates with the mouth-cavity by a hollow duct, even in the adult (comp. p. 155).

[3] A parietal foramen is, however, often present in the embryo, and persists throughout life in Callicthys.

·hypophysis and glandular saccus vasculosus are present, but these
vary much in the degree of their development.    The saccus
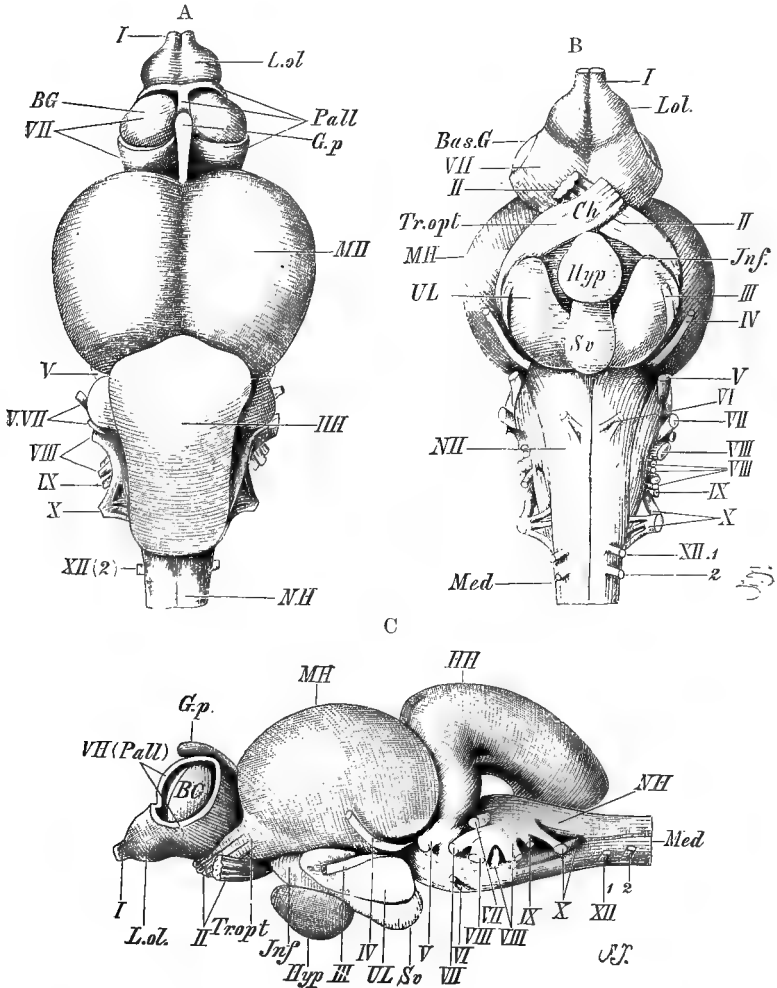


FIG. 133.—BRAIN OF SALMON. (A, dorsal ; B, ventral ; and C, lateral view.)

*VH*, prosencephalon ; *Pall*, pallium (in part removed), and *BG* and *Bas.G*, basal
    ganglia (corpora striata) of the prosencephalon ; *L.ol*, olfactory lobe ; *G.p*,
    pineal body ; *Jnf*, infundibulum ; *Hyp*, hypophysis ; *Sv*, saccus vasculosus ;
    *UL*, lobi inferiores ; *Tr.opt*, optic tract ; *Ch*, chiasma ; *MH*, mid-brain ;
    *HH*, cerebellum ; *NH*, medulla oblongata ; *Med*, spinal cord ; *I-X*, cranial
    nerves ; 1 and 2, first and second spinal nerves (the first represents the
    hypoglossal, *XII*).

vasculosus opens by several apertures into the infundibulum, and
is surrounded by a blood-sinus.

The mid-brain (Fig. 133) is extremely large relatively, while the thalamencephalon is depressed between it and the prosencephalon.

The extremely well-developed cerebellum is bent upon itself,
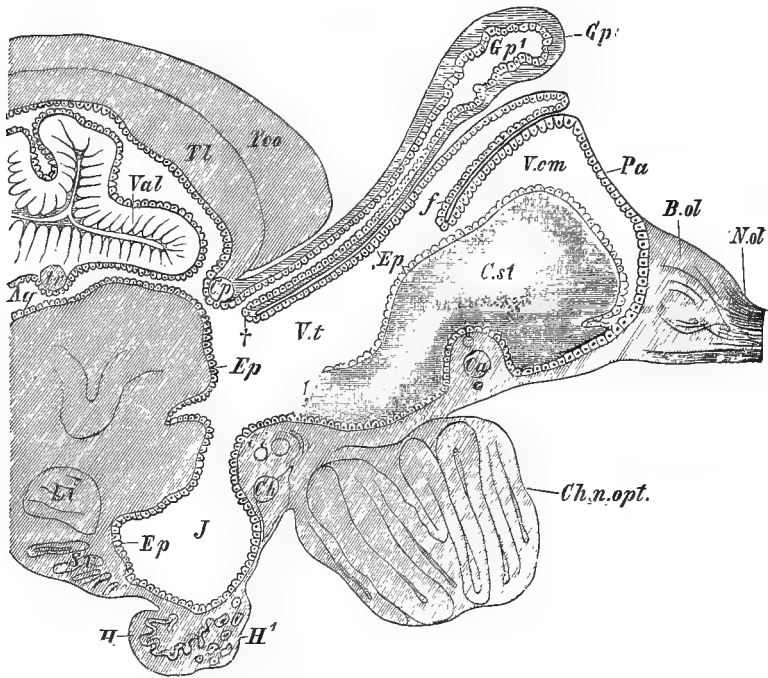


Fig. 134.—Longitudinal Vertical Section through the Anterior Part of the Teleostean Brain. (Founded on a figure of the Trout's brain by Rabl-Rückhard.)

*Tco*, roof of the optic lobes; *Tl*, torus longitudinalis; *Cp*, posterior commissure; *Gp*, pineal body, with a cavity (*Gp*[1]) in its interior; *Ep, Ep*, the epithelium (ependyme), lining the walls of the ventricles; †, point at which the epithelial roof of the secondary fore-brain (pallium, *Pa*) becomes continuous with the lining of the anterior wall of the pineal tube; at *f* is seen an outgrowth which represents a rudimentary parietal organ; *V.cm*, common ventricle (prosocœle) of the secondary fore-brain; *V.t*, third ventricle; *B.ol, N.ol*, olfactory lobe and nerve; *C.st*, corpus striatum, which lies on either side of the middle line; *Ch.n.opt*, optic chiasma; *Ci*, inferior commissure; *Ch*, horizontal commissure; *J*, infundibulum; *H, H*[1], hypophysis; *Sv*, saccus vasculosus; *Li*, lobi inferiores; *Aq*, aqueduct of Sylvius (mesocœle); *tr*, pathetic nerve; *Val*, valvula cerebelli.

overlies the medulla oblongata behind, and is prolonged in front into the ventricle of the mid-brain as a valvula cerebelli (Fig. 134), as is the case in Ganoids.

The Teleostean brain is of a specialised type. It has no direct

connection with that of Cyclostomes or Elasmobranchs, but has certainly passed through Ganoid-like stages.
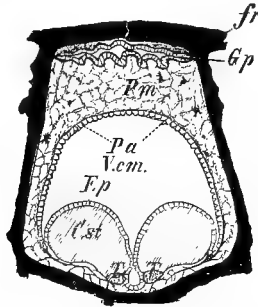


FIG. 135.—TRANSVERSE SECTION THROUGH THE FORE PART OF THE TELEOSTEAN BRAIN.

*fr*, frontal bone, underneath which the pineal tube, *Gp*, is visible in transverse section, and below this the pia mater, *Pm*; *Pa*, the pallium, or roof of the secondary fore-brain, formed of a simple epithelial layer; *V.cm*, prosocœle; *Ep*, ependyme; *T, T*, olfactory tracts at the base of the corpora striata (*C.st.*).

**Dipnoi.**—Both as regards external and internal structure, certain points of resemblance may be seen between the brain of Dipnoans and that of Elasmobranchs on the one hand and Amphibians on the other. This fact probably indicates that though the Elasmobranchii and Dipnoi have arisen from a common ancestral type, they have become differentiated along different lines.

The prosencephalon is well developed (Fig. 136): the thin pallium is mainly nervous, and is involuted along the median longitudinal line so as to completely separate the two hemispheres from one another in Protopterus: in Ceratodus they are united together posteriorly by a narrow commissure. Olfactory lobes arise from the prosencephalon anteriorly, and contain ventricles.

The thalamencephalon of Protopterus presents certain very characteristic features, especially as regards its roof. The pineal body has a long stalk, and its distal vesicle perforates the cartilaginous roof of the skull: in the embryo Ceratodus it even reaches as far as the integument. The choroid plexus gives rise to a vesicular organ, and as regards its



FIG. 136.—BRAIN OF *Ceratodus fosteri.* Dorsal view. (From Parker and Haswell's *Zoology*.)

*aud*, auditory nerve; *cbl*, cerebellum; *fac*, facial nerve; *gl*, glossopharyngeal; *med*, medulla oblongata; *mes*, mesencephalon; *oc*, oculomotor nerve; *opt*, optic nerve; *pros*, cerebral hemispheres; *rh*, olfactory lobes; *vg*, vagus nerve.

network of blood-vessels more nearly resembles that of Elasmobranchs than that of Amphibians. Lobi inferiores are present. Nervous and glandular portions can here also be recognised in the hypophysis.

The well-marked mid-brain is indistinctly paired in Ceratodus, but is unpaired in Protopterus.

The cerebellum is relatively much smaller than in Elasmobranchs and Teleosts, though better developed than in Urodeles: it gives rise to a valvula cerebelli.

**Amphibia.**—The prosencephalon of Amphibians is distinguished from that of Dipnoans by a higher development of the pallium, which, however, even in the latter group, is differentiated into an external layer of nerve fibres and an internal cellular layer. The basal ganglia (corpora striata) are less marked, and merely form a more or less prominent thickening of the wall of each hemisphere projecting into the lateral ventricle.

The Amphibian brain does not, however, lead towards that of Reptiles. Although the prosencephalon is more highly differentiated than in lower forms, the thalamencephalon and mesencephalon are simpler than in Fishes; and, on the whole, the brain of Amphibians is less complicated than that of any other Vertebrates.

In Urodeles the individual parts are more elongated and separated from one another than in Anurans, and the thalamencephalon is therefore more freely exposed. The hemispheres are almost cylindrical and are separated from one another by the pallial fold as far back as the anterior commissure,[1] as in Protopterus; while in the Anura (Figs. 137 and 138, A) they are fused together for a short distance anteriorly, where they are continuous with the olfactory lobes. The thalamencephalon and optic lobes are much broader in Anurans than in Urodeles. The cerebellum consists simply of a small transverse fold, and is especially rudimentary in Urodeles.

The infundibulum and hypophysis are well developed, but a saccus vasculosus is no longer so distinct as in Fishes, though traces of it can still be recognised. The epiphysis does not extend beyond the skull in Urodeles, but in Anuran larvæ it reaches the integument, undergoing reduction later, when the bony skull-roof is formed; indications, of its extracranial portion can, however, sometimes be recognised even in the adult (the "brow-spot" in .e.g., Rana temporaria): thus its intracranial portion does not represent the entire epiphysis. A parietal organ appears to be entirely wanting in all Amphibians with the exception of some few Anura in which traces of it have been described.[2]

In the Gymnophiona the olfactory lobes and hemispheres are

[1] The dorsal part of the anterior commissure has been said to represent a rudimentary *corpus callosum* (comp. note on p. 174, and Fig. 138, A).
[2] A parietal foramen was, however, present in the Palæozoic *Stegocephala* and other extinct Amphibians.

relatively larger than in other Amphibians, and the hemispheres overlap the posterior parts of the brain to a larger extent.
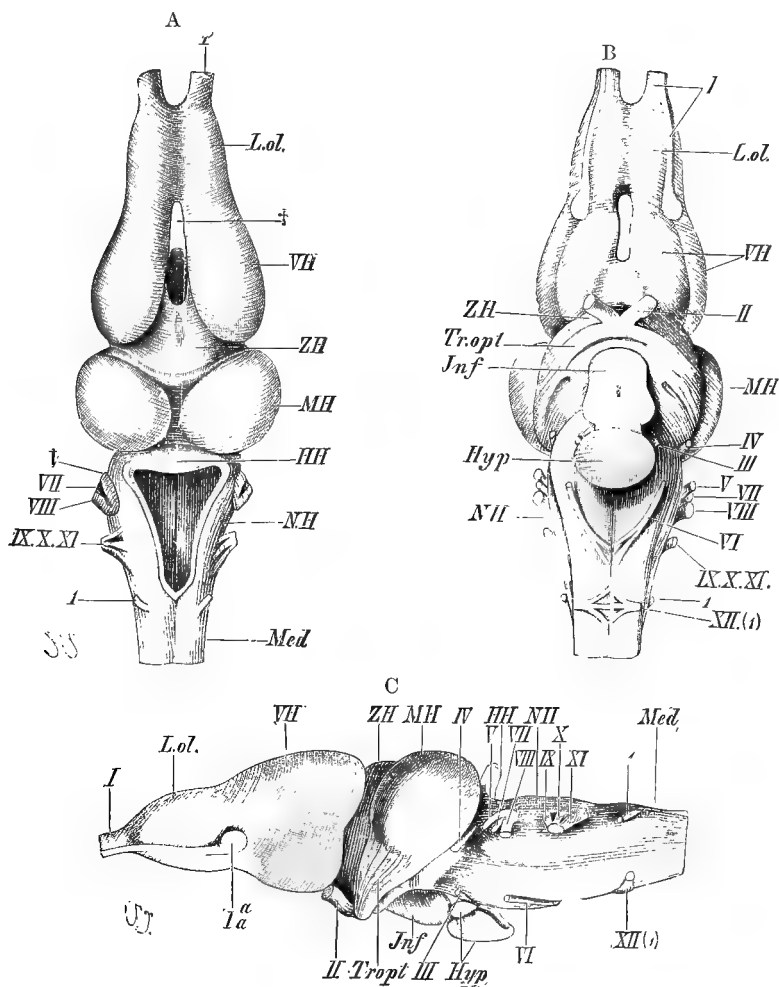


FIG. 137.—BRAIN OF *Rana esculenta.* (A, dorsal ; B, ventral ; and C, lateral view.)

*VH*, cerebral hemispheres ; *ZH*, thalamencephalon ; *MH*, mid-brain ; *HH*, cerebellum ; *NH*, medulla oblongata ; *Med*, spinal cord ; *I-X*, cranial nerves ; *Ia*, lateral root of olfactory nerve ; *XII* (1), ventral root of first spinal nerve (hypoglossal), and 1, its dorsal root ; *L.ol*, olfactory lobe ; †, space between the two hemispheres ; *Tr.opt*, optic tract ; *Jnf*, infundibulum ; *Hyp*, hypophysis.

**Reptiles.**—The brain of Reptiles reaches a considerably higher stage of development than that of the forms already described, and the individual parts overlie one another to a greater extent, especially in the Agamæ and Ascalabotæ.

The hemispheres are more highly developed, and the cortex is definitely differentiated and contains the characteristic pyramidal cells. In many cases also a distinct *hippocampal lobe* (Figs. 139, 140)
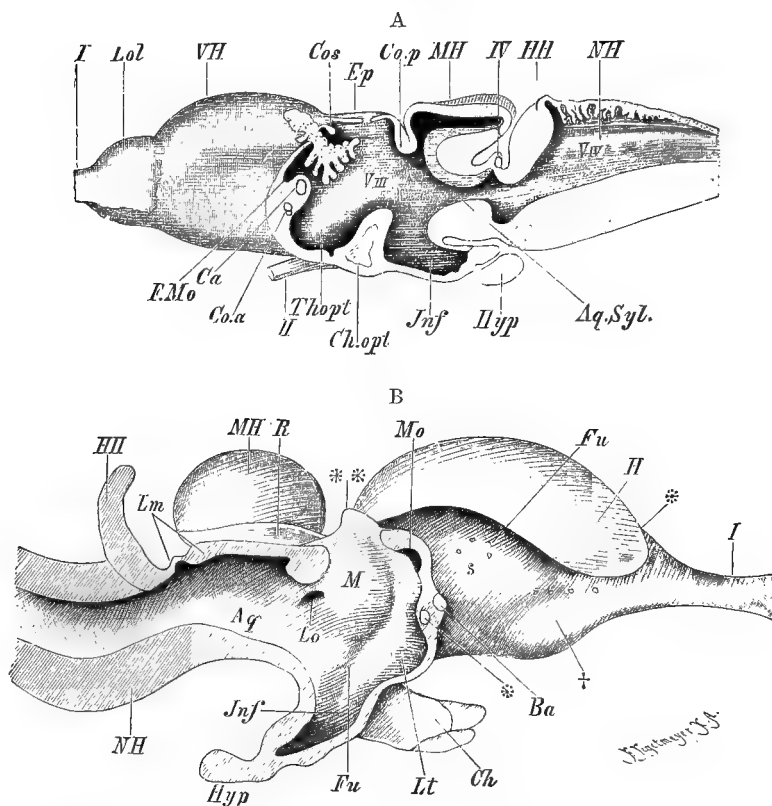


FIG. 138.—LONGITUDINAL SECTION THROUGH THE BRAIN OF A, *Rana*, AND B, *Hatteria*. (A after H. F. Osborn.)

*VH, MH, HH, NH*, prosen-, mesen-, meten-, and myelencephalon ; *H* in (B), hemisphere, which possesses a furrow on its median face, where it is perforated by numerous vascular foramina (*S*) : this furrow forms the boundary between the hemisphere and olfactory tract, the main root of which is seen at † ; *Lol*; olfactory lobe ; *I, II, IV*, origins of the olfactory, optic, and pathetic nerves ; *Ep*, **, base of epiphysis, which is not shown ; *Ch.opt* and *Ch*, optic chiasma ; *Lt*, lamina terminalis (the reference line should point to the cut edge below *Ba* and *), *Co.a*,* anterior commissure ; *Ca, Ba*, corpus callosum ; *F.Mo, Mo*, foramen of Monro, above which, in A, is seen the folded choroid plexus ; *Cos*, superior commissure ; *Co.p*, posterior commissure ; *VIII* and *VIV*, third and fourth ventricles ; *Th. opt* and *M*, optic thalamus ; *Lo* (in B), aperture, and *Fu*, furrow in the wall of the third ventricle ; *Aq, Aq.Syl*, aqueduct of Sylvius ; *Jnf*, infundibulum ; *Hyp*, hypophysis.

is present (Hatteria, Chelonia, Crocodilia), and the commissural system between the hemispheres known as the *fornix* as well as a so-called "*corpus callosum*" (comp. p. 174) are present in rudiment.
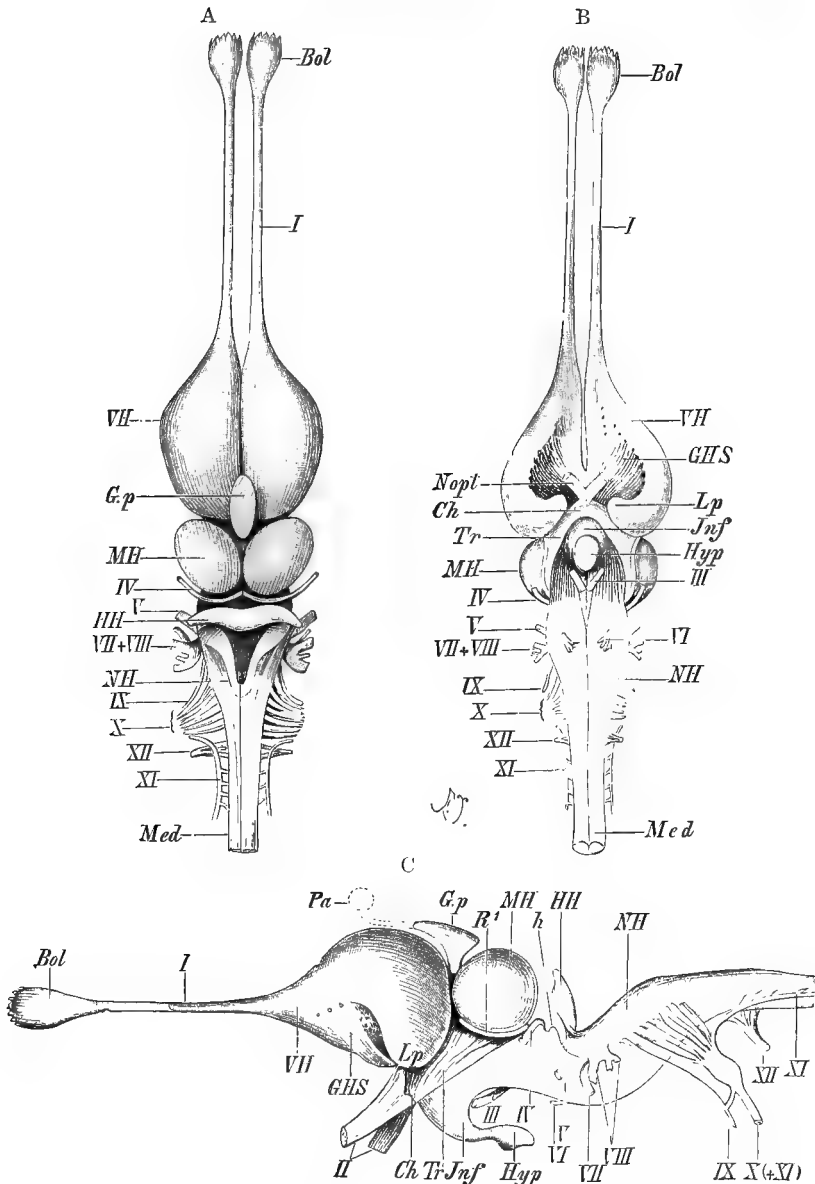
FIG. 139.—BRAIN OF *Hatteria punctata*. (A, dorsal; B, ventral; and C, lateral view.)

*VH, MH, HH, NH,* as in Fig. 138; *Med,* spinal cord; *I-XII,* cranial nerves; *Lp,* process of the hemisphere representing a hippocampal lobe; *N.opt,* optic nerve; *Ch,* optic chiasma; *Tr,* optic tract; *Jnf,* infundibulum; *Hyp,* hypophysis; *G.p,* pineal body, shown in C continuous with the parietal eye (*Pa*), and only indicated diagrammatically in A; *R¹,* curved ridge at the base of the optic lobe; *h,* small elevation in front of the cerebellum.
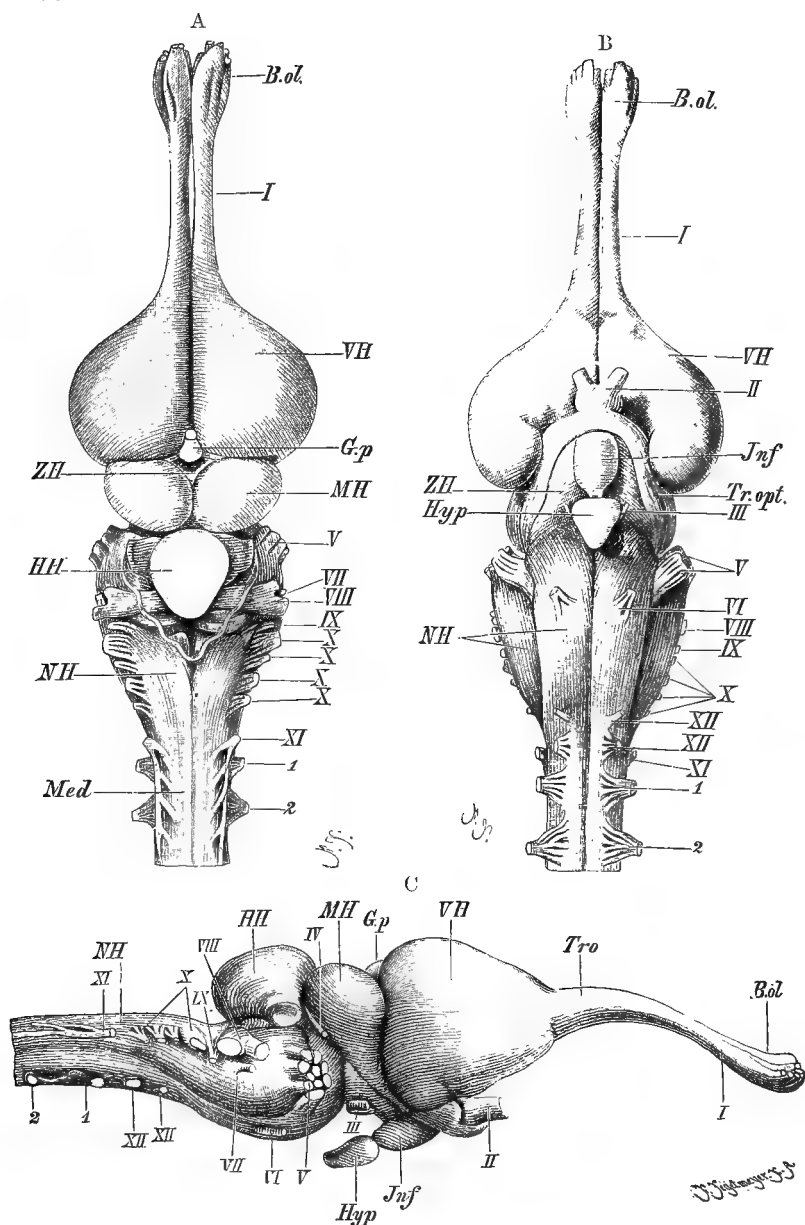
Fig. 140.—Brain of Alligator. (A, dorsal ; B, ventral ; and C, lateral view.)

*VH*, cerebral hemispheres, each of which gives rise postero-laterally to a hippo-
    campal lobe partially overlying the corresponding optic tract, *Tr.opt* ; *ZH*,
    thalamencephalon ; *MH*, optic lobes ; *HH*, cerebellum ; *NH*, medulla
    oblongata ; *I-XII*, cranial nerves ; 1, 2, first and second spinal nerves ; *B.ol*,
    olfactory bulb ; *Tro*, olfactory tract ; *G.p*, pineal body ; *Jnf*, infundibulum ;
    *Hyp*, hypophysis ; *Med*, spinal cord.

The olfactory lobes may be well marked or entirely invisible externally. In such forms as Anguis, Amphisbæna and Typhlops they are closely applied to the hemispheres, while in others (*e.g.*, Hatteria, Lacerta, Crocodilus) each consists of a well-marked olfactory tract, passing anteriorly into an olfactory bulb from which the nerves of smell arise. Olfactory ventricles are usually present.

The thalamencephalon is always depressed, and is hardly, or not at all, visible from the dorsal side. A distinct hypophysis and
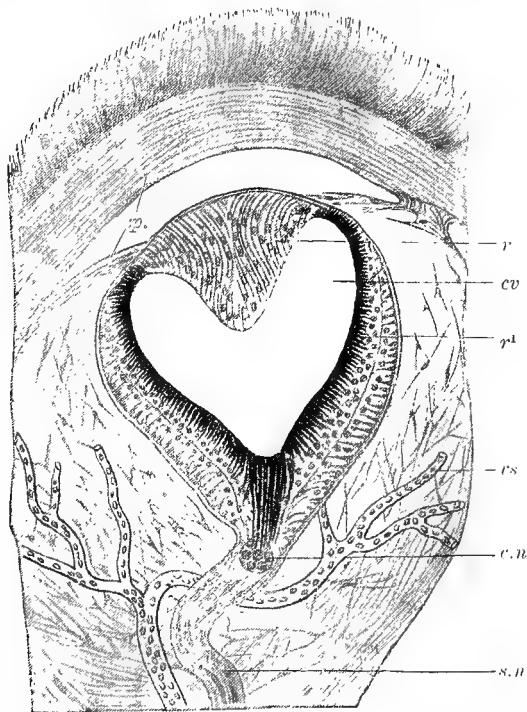


FIG. 141.—LONGITUDINAL SECTION THROUGH THE PARIETAL EYE AND ITS CON-NECTIVE-TISSUE CAPSULE OF *Hatteria punctata*. (After Baldwin Spencer.)

*cp*, connective-tissue capsule ; *r*, "lens ;" *cv*, cavity of the eye, filled with fluid ; *r*$^1$, retinal portion of the vesicle ; *vs*, blood-vessels ; *c.n*, cells in the nerve stalk (*s.n.*).

infundibulum as well as an epiphysis are present, and in Lizards the parietal organ retains more or less distinctly, even in the adult, its primitive structure as a median eye.

This *parietal eye* (Fig. 141) is situated in the parietal foramen of the skull, and is in close connection with the epiphysis, though in the embryo the nerve which supplies it is seen to arise independently from the brain, in front of the pineal outgrowth. The eye has the form of a vesicle, the dorsal wall of which may become thickened to form a transparent lens-like body, while the rest of

the wall consists of several layers and forms a pigmented retina, with which the more or less rudimentary nerve is continuous.  The vesicle is surrounded externally by a connective-tissue capsule, and in many cases the integument and connective-tissue immediately overlying the vesicle is pigmentless and transparent, forming a kind of cornea.  Traces of a vitreous body have also been observed. Various degrees of reduction of the different parts as they occur *e.g.*, in Hatteria (Fig. 141), are seen amongst Lizards.  (See also p. 155).  Traces of a parietal eye, with lens and pigment, have also been observed in the embryo of the Viper (Pelias berus).

In the mid-brain the two well-marked optic lobes may show indications of a further subdivision into four ; from them the optic tracts pass downwards and forwards to the chiasma.  The cerebellum is relatively small, except in the Crocodilia (Fig. 140), in which it consists of a thicker median, and two lateral portions, while in other Reptiles, and more particularly in Lizards, it is not much more highly developed than in Amphibians.  The medulla oblongata has a marked ventral flexure.

**Birds**.—The basal ganglia (corpora striata) of the hemispheres reach a relatively larger size in Birds than in any other Vertebrates, while the differentiation of the cortex and commissures does not show any marked advance on that seen in Reptiles.

The different parts of the brain overlie one another much more markedly than in any Reptile, and the hemispheres are much larger relatively, covering over the thalamencephalon and part of the mid-brain (Fig. 142).  The olfactory lobes are short and conical.  The distal, enlarged end of the pineal body extends as far as the dura mater, and the structure of the internal part of the organ resembles that of a tubular gland, penetrated by fibrous tissue and blood-vessels.  There is no trace of a parietal organ.

The cerebellum consists of a well-developed and folded median lobe, and of two lateral portions (flocculi), which vary much both in form and size.  Posteriorly it completely covers the fourth ventricle. The two optic lobes are separated from one another and pressed downwards, so as to lie on the sides of the brain in the angle between the hemispheres, cerebellum, and medulla oblongata, and they are connected by a broad commissure.  The ventral side of the hindbrain shows a marked flexure, bending upwards to the spinal cord.

**Mammals**.—The brain in embryo Mammalia is very similar to that of the Sauropsida, but its later differentiation—more particularly that of the pallium—gives it a very special character. The cortex becomes much more highly differentiated, and in many Mammals is more or less highly convoluted (Figs. 144, 146), giving rise to gyri and sulci (p. 154).  In others, again, the surface of the hemispheres remains smooth (Fig. 143), but a subdivision into lobes (frontal, parietal, temporal, &c.) can always be recognised to a greater or less extent, and the hemispheres are relatively so large as to cover over the more posterior parts of the brain ; in some of the lower forms, the mid-brain can still be seen
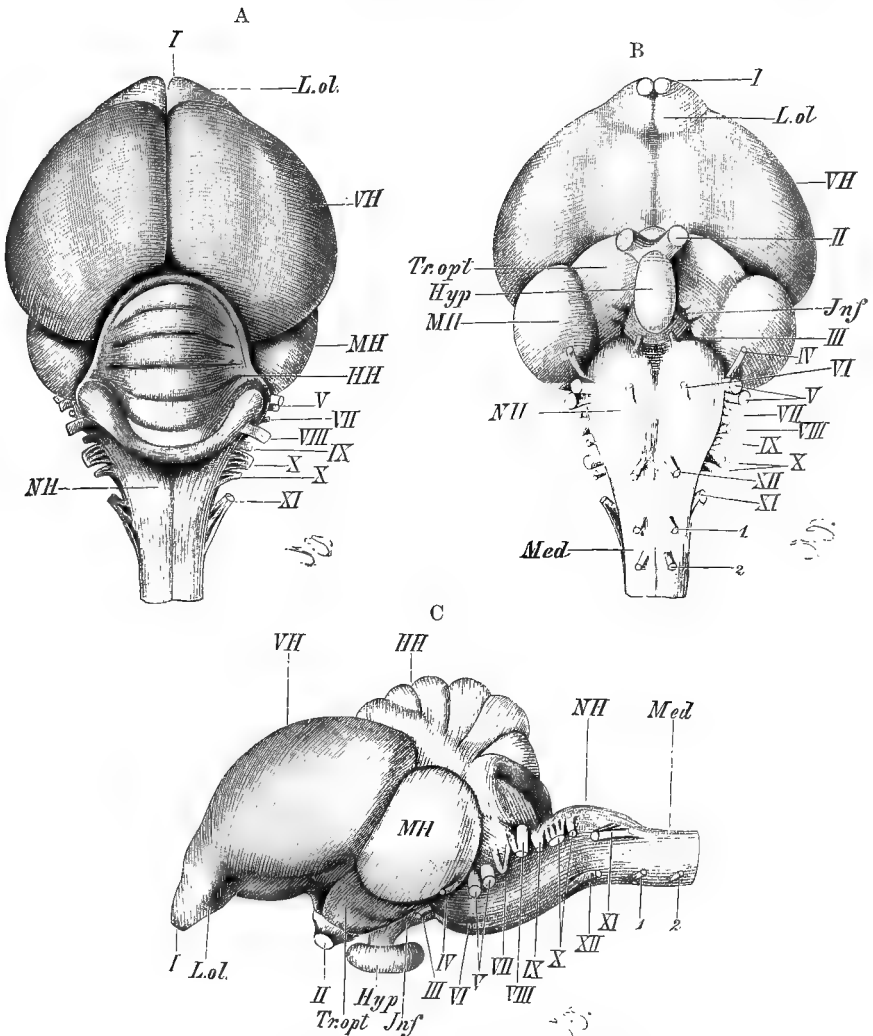
FIG. 142.—BRAIN OF PIGEON. (A, dorsal; B, ventral; and C, lateral view.)

*VH*, cerebral hemispheres; *MH*, optic lobes; *HH*, cerebellum; *NH*, medulla oblongata; *Med*, spinal cord; *I-XII*, cranial nerves; 1, 2, first and second spinal nerves; *L.ol*, olfactory lobes; *Tr.opt*, optic tract; *Jnf*, infundibulum; *Hyp*, hypophysis.

from above (Fig. 143) while in the higher types (Primates) even part of the cerebellum is hidden (Figs. 145, 146).

The commissures between the hemispheres (*corpus callosum* and *fornix*, Fig. 145) are also much more highly developed than in the Sauropsida. The corpus callosum or pallial commissure, though small in the lower Mammalia (*c.g.*, Monotremes and

Marsupials),[1] is usually a large and important structure; its relative size is in inverse proportion to that of the anterior commissure. In addition to the anterior and posterior commissures, a middle commissure is definitely differentiated from the
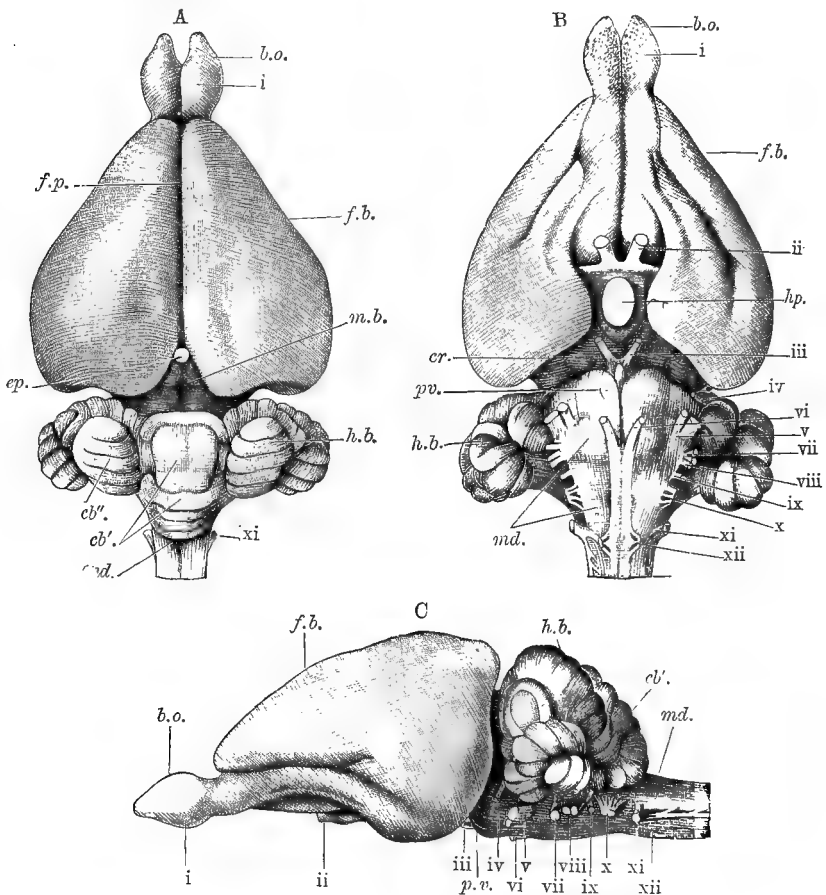


FIG. 143.—BRAIN OF RABBIT. (A, dorsal; B, ventral; and C, lateral view.)

*f.b.*, cerebral hemispheres; *m.b.*, optic lobes; *h.b.*, cerebellum; *c.b'.*, superior vermis, and *c.b''.*, lateral lobe of cerebellum; *md.*, medulla oblongata; *ep.*, pineal body; *h.p.*, hypophysis; *pv.*, pons Varolii; *cr.*, crura cerebri; *f.p.*, pallial fissure; *b.o.*, olfactory bulb; *i-xii*, cerebral nerves.

base of the brain as a distinct structure connecting the two optic thalami.

In correspondence with the division of the hemispheres into lobes, there is a marked differentiation of the lateral ventricles,

[1] Recent researches indicate that a true corpus callosum is present only in the Placentalia, and that the commissure which is usually supposed to represent it in lower types may be more correctly described as the *hippocampal commissure*.

so that an *anterior*, a *posterior*, and an *inferior cornu* can be distinguished in each; the inferior cornu extends into what corresponds to the hippocampal lobe of Reptiles (p. 168), and an eminence on its floor, known as the *hippocampus major*, is much more marked than in lower forms. The olfactory lobes, in which an olfactory
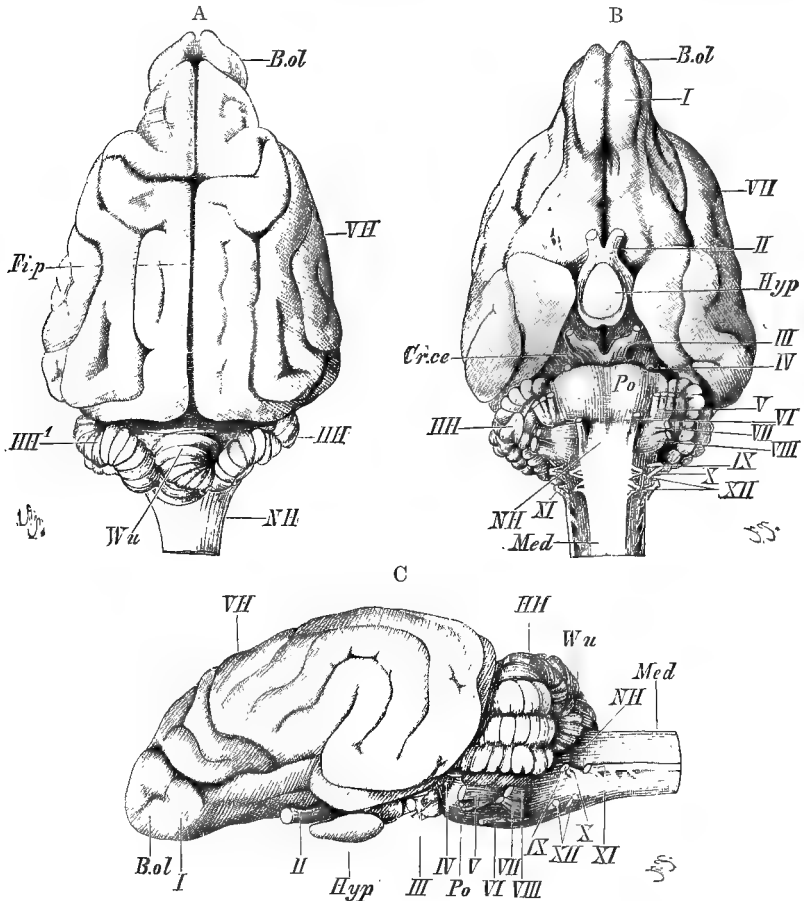


FIG. 144.—BRAIN OF DOG (POINTER). (A, dorsal; B, ventral; and C, lateral view.)

*VH*, cerebral hemispheres; *MH*, optic lobes; *HH*, cerebellum, *Wu*, superior vermis; *HH*¹, lateral lobe of cerebellum; *NH*, medulla oblongata; *Med*, spinal cord; *Hyp*, hypophysis; *Po*, pons Varolii: *Cr.ce*, crura cerebri; *Fi.p*, pallial fissure; *B.ol*, olfactory bulb; *I-XII*, cranial nerves.

tract and bulb can be distinguished, usually extend forwards freely from the base of the prosencephalon and each may (*e.g.*, Horse) contain a prolongation of the lateral ventricle; but in some cases (*e.g.*, numerous aquatic forms and Primates) they are completely covered by the frontal lobes.

The pineal body is displaced downwards by the hemispheres and lies against the anterior part of the mid-brain, not reaching to the roof of the skull.  Its bifurcated peduncle connects it
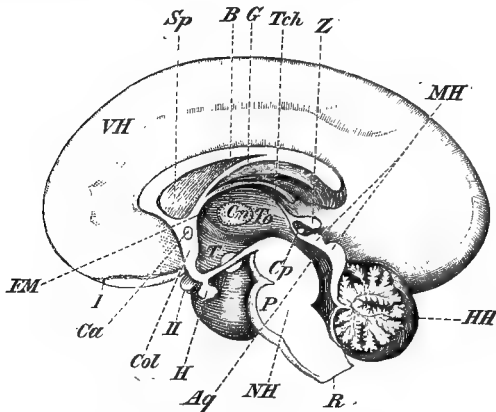


FIG. 145.—HUMAN BRAIN.  (Median longitudinal vertical section.)
(Mainly after Reichert.)

*VH*, cerebrum ; *To*, optic thalamus (thalamencephalon), with the middle commissure (*Cm*) ; *Z*, pineal body ; *T*, infundibulum ; *H*, pituitary body ; *MH*, corpora bigemina, with the aqueduct of Sylvius (*Aq*), anterior to which is seen the posterior commissure (*Cp*) ; *HH*, cerebellum ; *NH*, medulla oblongata, with the pons Varolii (*P*) ; *R*, spinal cord ; *B*, corpus callosum ; *G*, fornix, which extends antero-ventrally to the lamina terminalis (*Col*), in the upper part of which is seen the anterior commissure (*Ca*), and between the latter and the optic thalami (*To*) the foramen of Monro (*FM*) ; *Tch*, tela choroidea ; *I*, olfactory nerve ; *II*, optic nerve.
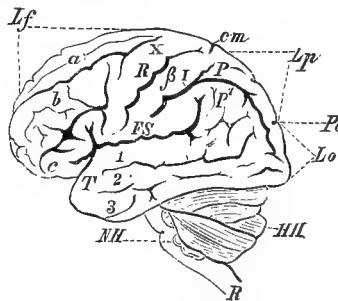


FIG. 146.—CONVOLUTIONS OF THE HUMAN BRAIN.  (After A. Ecker.)

*Lf*, frontal lobe ; *Lp*, parietal lobe ; *Lo*, occipital lobe ; *T*, temporal lobe ; *a*, *b*, *c*, superior, middle, and inferior frontal gyri ; *X*, *β*, anterior and posterior central convolutions, separated from one another by the fissure of Rolando (*R*) ; *cm*, the calloso-marginal sulcus on the dorsal surface ; *P*, *P*$^1$, superior and inferior parietal gyri separated from one another by the interparietal fissure (*I*) ; *Po*, parietal-occipital fissure ; *FS*, Sylvian fissure ; 1 to 3, superior, middle, and inferior temporal convolutions ; *HH*, cerebellum ; *NH*, medulla oblongata ; *R*, spinal cord.

with the roof of the thalamencephalon and contains nervous substance ; its distal end has the form of a rounded or oval sac, consisting of compact epithelial tissue and containing concretions.  No indication of a parietal organ can be recognised.

Traces of the saccus vasculosus and lobi inferiores still occur, even in Man, in connection with the infundibulum.

The mid-brain is of smaller relative size than in other Vertebrates. A transverse furrow across the solid optic lobes sub-divides them into an anterior larger and a posterior smaller pair of lobes (comp. p. 172).

The division of the cerebellum into a median and two lateral portions, already indicated in Reptiles, but much more plainly marked in Birds, is carried to a still further extent in Mammals. The median portion gives rise to the so-called *superior vermis* while the lateral parts form the *lateral lobes* and *flocculi* (Figs. 143, 144). The two lateral lobes are connected by a large commissure, the *pons Varolii* (Figs. 143–145) : this extends round the medulla oblongata ventrally, and is more largely developed the higher we pass in the Mammalian series. Other bands of nerve-fibres connecting the cerebellum with other parts of the brain are spoken of as anterior, middle, and posterior peduncles of the cerebellum.

The brain in Cretaceous Birds (*e.g.*, Hesperornis) and in Tertiary Mammals (*e.g.*, Dinoceras, Triceratops) was much less highly developed, and the hemispheres relatively much smaller, than in existing forms.

## II. PERIPHERAL NERVOUS SYSTEM.

Two principal groups of peripheral nerves may be distinguished, viz., **spinal** and **cerebral**, that is, those which arise from the spinal cord and brain respectively : by their means a physiological connection is established between the periphery of the body and the central nervous system both in centripetal and centrifugal directions. The spinal nerves retain the more primitive and simple relations, and all show a similar arrangement along both dorsal and ventral regions of the spinal cord, so that each segment of the trunk possesses a *dorsal* and a *ventral pair*. The former consists of *sensory*, the latter of *motor* fibres (Fig. 147).

Each dorsal or sensory nerve has a *ganglion* in connection with it, while in the ventral nerves a ganglion is wanting, at any rate in the adult. The ventral nerves arise as direct outgrowths from the spinal cord, while the dorsal nerves first appear as outgrowths from their ganglia, coming into connection with the cord secondarily. The ganglia themselves are developed from a *neural ridge* of epiblast cells lying close to the junction of the medullary cord (p. 149) and outer epiblast. On the distal side of each ganglion, both nerve-roots almost always become bound up in a common sheath, though many facts seem to indicate that in the ancestors of existing Vertebrates the dorsal and ventral
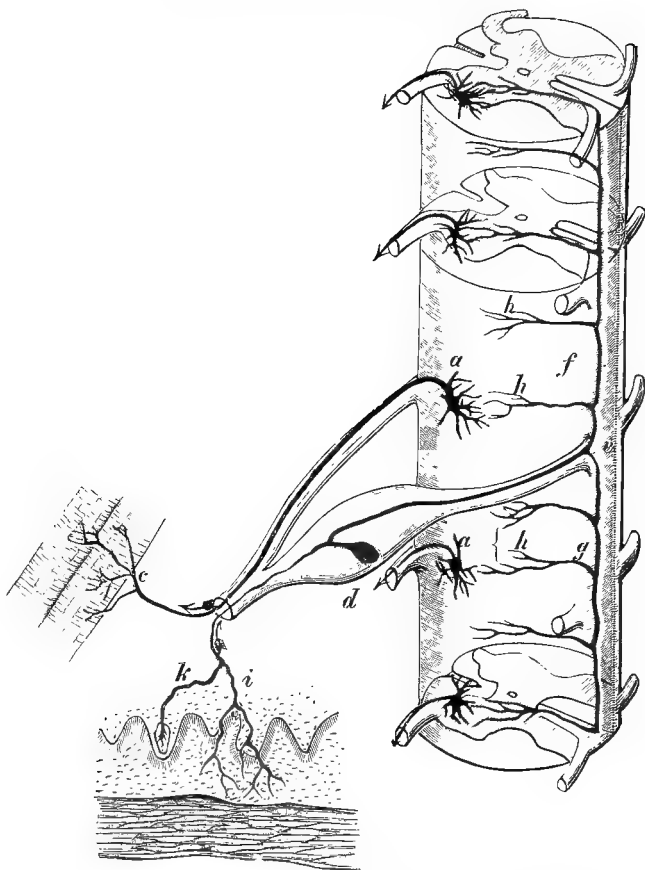
Fig. 147.—Diagram illustrating the Origin, Course, and Termination of the Motor and Sensory Fibres of the Spinal Nerves, as well as the Relations of the Sensory Collateral Fibres to the Points of Origin of the Ventral Roots.    (After M. V. Lenhossék.)

The spinal cord is shown as if transparent.    The fibres of the ventral roots arise from the cells of the motor ventral cornua of the gray matter (a) and end in fine branches on the striated muscle fibres (c).    The spinal ganglion (d) is shown relatively much larger than in reality, and in it only a single unipolar nerve-cell is represented : the centripetal fibre of the latter is seen entering the dorsal root, and at e bifurcates in the spinal cord into an anterior (f) and a posterior (g) branch, each of which ends freely in the gray substance, first giving off numerous collateral fibres (h).    The centrifugal fibre of the cell in the spinal ganglion forms a peripheral sensory fibre extending to the skin, where part of it is shown ending in fine branches in the epidermis (i), another part forming a coil in connection with a tactile corpuscle (k).

roots remained distinct, as, in fact, is still the case in Amphioxus and Petromyzon.

The common *nerve-trunk* formed by the junction of the two

roots divides up again into a *dorsal*, a *ventral*, and a *visceral branch*. The first of these goes to the muscles and skin of the back, the second supplies the lateral and ventral portions of the body-wall, while the intestinal branch comes into connection with the *sympathetic* (p. 188).

## 1. **SPINAL NERVES.**

As a general rule, each corresponding pair of dorsal and ventral roots lies in the same transverse plane : an exception to this is seen, however, in Amphioxus,[1] Cyclostomes, Elasmobranchs, and Dipnoans, in which the mesoblastic somites of the right and left side are arranged alternately, and thus the points of exit of the nerve-roots also alternate right and left, or each ventral pair alternates with a dorsal pair. In Ganoids also, lateral displacements of the nerve-roots are met with.

In Fishes the greatest variations are seen as regards the mode of exit of the nerves (which pass through the intercalary pieces of the vertebral column, through the arches, or between them); but from the Amphibia onwards the nerves always make their exit on each side *between* the arches, through the intervertebral foramina.

In their primitive undifferentiated condition the spinal nerves have a strictly metameric arrangement, and are equally developed in all regions of the body. As already pointed out in the section on the spinal cord, this condition becomes modified by the development of the appendages, so that a number of spinal nerves unite together to form **plexuses**, which, according to their position, are spoken of as *cervical, brachial, lumbar,* and *sacral* (Fig. 121). The number of nerves composing these corresponds to the number of body-segments taking part in the formation of the appendages, and their relative size is usually directly proportional to the development of the latter.

In contrast to Fishes, the great variation in the plexuses of which renders it impossible to reduce them to a common plan, we find from the Amphibia onwards a typical grouping of the branches of the *brachial plexus*, from which numerous nerves arise supplying the shoulder and fore-limb dorsally and ventrally (e.g., *thoracic, subscapular, axillary, radial, musculo-cutaneous,* and *ulnar*). The *lumbo-sacral plexus* shows in general, and more particularly in Mammals, much greater variations than does the brachial plexus. The nerves arising from it are also arranged in a dorsal and a ventral series, the larger ones being spoken of as the *obturator,*

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[1] In Amphioxus both the dorsal and ventral nerves innervate muscles, and it appears that in many of the Craniata also the dorsal roots are not purely sensory.

*crural, sciatic,* and *pudendic.* The sciatic divides up in the hind-limb into a *tibial* and a *fibular* nerve.[1]

## 2. CEREBRAL NERVES.

The following twelve pairs of cerebral nerves can be distinguished, and of these the eleventh pair are plainly differentiated only in the Amniota, and the twelfth are represented by the first spinal nerves in certain Fishes and in all Amphibians :—

       I.   Olfactory.
      II.   Optic.
    III.   Oculomotor.
    IV.   Pathetic or trochlear.
     V.   Trigeminal.
    VI.   Abducent.
   VII.   Facial.
  VIII.   Auditory.
    IX.   Glossopharyngeal.
     X.   Vagus or pneumogastric.
    XI.   Spinal accessory.
   XII.   Hypoglossal.

In their mode of early development the cerebral nerves resemble the spinal nerves in many respects (p. 177), and a gradual transition between the two groups is indicated in the lower Vetebrata. Certain of them, like the motor spinal nerves, arise as direct ventral outgrowths from the embryonic brain (III, VI, XII, and probably IV[2]). Others, again (V and VII in part, VIII, IX, and X), arise dorsally, primarily in connection with their individual ganglia and becoming actually connected with the brain secondarily : these must therefore, so far as they consist of sensory, centripetal elements, be looked upon as homodynamous with the dorsal roots of the spinal nerves. But it must be borne in mind that all these nerves, with the exception of the olfactory, optic, and auditory, are of a mixed character, containing motor as well as sensory fibres ; and a further difference between them and the dorsal roots of the spinal nerves (comp. note on p. 179) is seen in the shifting of their origin to the ventral side of the brain during development.

A study of development shows that portions of the epiblast lying peripherally to the brain take part in the formation of the ganglia of the trigeminal, facial, auditory, and vagus nerves, and that each definitive

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[1] In animals in which the extremities have disappeared, all traces of the corresponding plexuses have also usually vanished : Snakes, however, still retain remnants of them.

[2] The fourth nerve is peculiar in appearing from the dorsal surface of the brain, but this is probably a secondary condition p. 184).

ganglion consists of a primary "*spinal*" ganglion and of a more peripheral *lateral* ganglion in connection with the nerve, from which latter an *epibranchial* ganglion arises from the epiblast dorsally to the region of the gill-clefts, and takes part in the formation of the terminal branches of the nerve. The presence of an epibranchial ganglion on the trigeminal may indicate the former presence of a gill-cleft in this region.

It must be remembered that the head is primitively composed of a series of metameres (p. 66), and it is therefore important to ascertain, as far as is possible in the present state of our knowledge, to which individual metameres the different cranial nerves belong. The olfactory and optic nerves present certain peculiarities which bring them under another category, and they will be treated of later in connection with the corresponding sensory organs.

The following general summary gives a scheme of the probable primitive relations of the head-segments and cerebral nerves, founded mainly on the conditions existing in Elasmobranch embryos.

TABLE SHOWING THE SEGMENTAL ARRANGEMENT OF THE CEREBRAL NERVES, WITH THEIR RELATION TO THE METAMERES OF THE HEAD.

| | Ventral branch. | Dorsal branch. |
|---|---|---|
| 1st *Metamere* (superior, inferior, and anterior rectus, and inferior oblique muscle).[1] | Oculomotor (*III*). | Ramus ophthalmicus profundus of the trigeminal (*V*), together with the ciliary ganglion. |
| 2nd *Metamere* (superior oblique).[1] | Trochlear (*IV*). | Trigeminal (with its ganglion, *minus* the ramus ophthalmicus profundus). |
| 3rd *Metamere* (posterior rectus).[1] | Abducent (*VI*). | Facial (*VII*), and auditory (*VIII*), with their ganglia. |
| 4th *Metamere* (muscles which are early aborted). | Wanting. | |
| 5th *Metamere* (muscles which are early aborted). | Wanting. | Glossopharyngeal (*IX*), with its ganglion. |
| 6th and 7th *Metameres* (part of the most anterior region of the large trunk-muscles). | Appears to be wanting. | Vagus (*X*), with its ganglia. |
| 8th and 9th *Metameres* (anterior part of trunk-muscles). | Ventral roots of the hypoglossal. | Vestigial dorsal roots of the hypoglossal (*XII*), usually only present in the embryo. |

Figures 148 and 149 illustrate the distribution of the cerebral nerves in adult aquatic and terrestrial Vertebrates respectively (comp.

[1] It is possible, however, that these eye-muscles belong, not to the somites, as stated on pp. 133 and 143, but to the visceral muscles.

Fig. 148.—Diagram showing the Distribution of the Cerebral Nerves in the Water-breathing Anamnia.

*Cav; nas*, olfactory organ; *A*, eye; *Pal.Quadr*, palatoquadrate; *Mand*, mandible; *S*, spiracular (hyoid) cleft; *I-V*, branchial clefts. *I*, olfactory nerve; *II*, optic nerve; *III*, oculomotor nerve; *IV*, pathetic nerve; *VI*, abducent nerve. The other cerebral nerves are distinguished by different kinds of shading.

*Oblique shading.* The nerves supplying integumentary sense-organs (lateral line branches of *VII* and *X*), all of which, as well as the auditory nerve (*VIII*) arise from the same centre (*Centr*). They are as follows:—*Oph.sup.VII*, superficial ophthalmic branch of facial, with its ganglion (*Gos*); *Bucc.VII*, buccal branch of facial, with its ganglion (*Gb*); *Mand.ext.* † *VII* and †† *VII*, anterior and posterior twigs of the external mandibular branch of facial, with its ganglion (*G.lat.*); *Lat.X*, lateral line branch of vagus, with its ganglion (*G.lat*). The last-mentioned nerve gives rise to supratemporal branch (*Supt*), and in Dipnoi is connected with the lateral line branches of the facial by a commissure (*Co.lat*).

*Black.*—Trigeminal (*V*), with its three main branches: *Oph.prof.V*, deep ophthalmic (profundus); *Max.V*, maxillary; *Mand.V*, mandibular, giving off motor twigs at *P.m.v.*; *R.m.v*, small branch (? = superficial ophthalmic).

*Dotted.*—Facial (*VII*). *Pal.VII*, palatine; *Ch.ty*, chorda tympani (internal mandibular); *Hy.Ma.VII*, hyomandibular, giving off branches to visceral muscles (*M, M, M, M*).

*Transverse shading.*—Auditory (*VIII*).

*Dark gray.*—Glossopharyngeal (*IX*), which forks (*pr, po*) over the 1st branchial cleft, gives off anteriorly a palatine (*Pal. IX*) and a pharyngeal branch (broken line), and is connected with the facial by the anastomosis of Jacobson (*Jak*).

*Lighter gray.*—Vagus (*X*), which gives off branchial branches (*X*) over the remaining clefts, each of which subdivides into a smaller anterior (*pr*) and a larger posterior (*po*) twig; *Int.X*, visceral branch.

*White.*—Spinal nerves which pass out through the skull and possibly correspond to the hypoglossal of higher Vertebrates; *Id, IId*, and *Iv, IIv*, dorsal and ventral roots of the first two spinal nerves.

FIG. 149.—DIAGRAM SHOWING THE DISTRIBUTION OF THE CEREBRAL NERVES IN THE AMNIOTA.

*Ol*, olfactory organ; *A*, eye; *Ol*, tympano-eustachian passage; *Mand*, mandible; *Z*, tongue. The other nerves are distinguished by different kinds of shading, to correspond with Fig. 148.

*I*, olfactory nerve; *II*, optic nerve; *III*, oculomotor nerve; *IV*, pathetic (trochlear) nerve; *VI*, abducent nerve.

*V*, trigeminal, with its three branches; the ophthalmic (*Oph.V*), maxillary (*Max.V*), and mandibular (*Mand.V*), the last-named dividing into a mandibular in the narrower sense (*Mn*), and a lingual (*Ling.V*). The latter is connected with a motor portion (*P.m.V*) and with the chorda tympani branch of the facial (*Ch.ty*);

*Me at*, branches to chin; *Biv*, *Mn*, motor branches which supply the ventral belly of the biventer and the mylohyoid muscles; *Au*, auriculo-temporal branch.

*VII*, facial; *G*, geniculate ganglion; *Pet*, major superficial petrosal nerve, which arises from the sensory portion of the facial, and extends forwards beyond the spheno-palatine ganglion (*tt*) as the palatine (*Pal.VII*); *Ch.ty*, chorda tympani, part of which in Mammals extends through the middle ear (*Ot*); *Hy.Mx.VII*, main (hyomandi-bular) trunk, which in Primates gives rise to the plexus (*M/m*) for the facial muscles; *M*, *M*, branches to the muscles of the ear and to the visceral muscles; *P.im*, intermediate portion of facial.

*VIII*, auditory nerve.

*IX*, glossopharyngeal. *Ling.IX*, lingual, and *Phar.IX*, pharyngeal branch; *Jak*, anastomosis of Jacobson, connecting the glossopharyngeal and facial nerves.

*X*, vagus. *Int.X*, intestinal branch, with its further subdivisions, R, R, R, R.

*XI*, spinal accessory.

*XIIc*, hypoglossal; *XIId*, its vestigial dorsal roots.

*Id*, *IId*, and *Iv*, *IIv*, dorsal and ventral roots of the first two spinal nerves.

*Ganglia derived from the sympathetic.* †, ciliary; ††, sphenopalatine, which is connected with the facial by the superficial petrosal nerve; * otic, connected with the facial and glossopharyngeal by the anastomosis of Jacobson; **, submaxillary, perforated by the chorda tympani nerve.

also Fig. 121). The ganglia belonging to the cerebro-spinal system are shown in both figures, those belonging to the sympathetic in Fig. 149 only.

**Nerves of the Eye-muscles.**—The **oculomotor** (III) **trochlear** or **pathetic** (IV) and **abducent** (VI) **nerves** (Figs. 148 and 149) supply the muscles which move the bulb of the eye as shown in the table on p. 181. The oculomotor arises from the base of the mid-brain, and comes into secondary connection with an oculomotor or *ciliary ganglion* which primarily belongs to the sympathetic system.

The trochlear nerve, although actually arising in the interior of the ventral part of the mid-brain, appears externally on the dorsal side of the anterior margin of the hind-brain (valve of Vieussens p. 156). Primitively it contains sensory as well as motor fibres, and these in Fishes and Amphibians supply the connective-tissue of the eye and the endocranium.

The abducent nerve, which arises far back on the floor of the medulla oblongata, also probably contains mixed fibres in the Anamnia. In the Anura it becomes closely connected within the skull with the Gasserian ganglion of the trigeminal.

**Trigeminal Nerve.**—This is one of the largest of the cerebral nerves. It arises from the ventro-lateral region of the anterior part of the medulla oblongata by a large lateral sensory and a small ventral motor root, has a large intra- or extra-cranial *Gasserian ganglion* at the origin of the former and then, in Fishes (Fig. 148), divides into two main branches, an *ophthalmic* (including a *superficial* and a *deep* or *profundus* portion), and a *maxillo-mandibular* : in most terrestrial forms (Fig. 149) the maxillary and mandibular nerves arise separately. From the presence of these three characteristic branches, often known as the *first, second,* and *third divisions* of the trigeminal, its name is derived. It passes out from the skull sometimes through a single aperture, and sometimes by two or even three distinct ones.

The superficial branch of the first division is usually distinct in Fishes and Dipnoans and probably also in Urodeles, and passes dorsally over the eye-ball, the deep branch passing below the superior and anterior recti and superior oblique muscles. In other Fishes and in higher forms the two branches appear to be united. It supplies the integument of the forehead and snout as well as the eye-ball, eye-lids and conjunctiva, branches apparently going to the lachrymal glands when present : it is entirely sensory. A consection of the profundus with the ciliary ganglion arises secondarily.

The second division of the trigeminal, which is also a sensory nerve and with which a *sphenopalatine ganglion* derived from the sympathetic is connected, extends first along the floor of the

orbit, supplying the lachrymal and Harderian glands, when present, as well as the roof of the mouth; it then passes to the upper jaw, supplying the teeth; and finally, as the infraorbital branch, perforates the skull to reach the integument in the region of the upper jaw, snout, and upper lip.

The third division of the trigeminal is of a mixed nature; it supplies on the one hand the masticatory muscles and several muscles on the floor of the mouth, and also gives rise, from Amphibians onwards, to the great sensory nerve of the tongue (lingual or gustatory nerve); while another branch, passing through the inferior dental canal, supplies the teeth of the lower jaw, and then gives off one or more branches to the integument of the latter and of the lower lip. Two ganglia, the *submaxillary* and the *otic* (Fig. 149), derived from the sympathetic, are connected with its mandibular division (sensory portion).

**Facial nerve.**—This, which is also a mixed nerve, originally possesses two distinct ganglia in connection with its sensory and mixed portion (Fig. 148) : these can be recognised up to Urodeles, but in the course of development one of them gradually comes into connection with the ganglion of the trigeminal, and in Anura is indistinguishable from it. The other—known as the *geniculate ganglion*—is retained in all Vertebrates, in connection with its mixed root (Fig. 149).

The facial nerve consists primarily (in aquatic Vertebrates) of the following main branches (Fig. 148) :—

I. A system of sensory branches for the supply of the integumentary sense-organs of the head (p. 190),[1] as follows :—(*a*) a *superficial ophthalmic*, running parallel to and usually accompanying the corresponding branch of the trigeminal; (*b*) a *buccal*, which gives off an *otic* branch; and (*c*) an *external mandibular* ( = part of the hyomandibular, see below).

II. A sensory (*a*) *palatine*, anastomosing with the maxillary branch of the trigeminal, and (*b*) *internal mandibular* or *chorda tympani*.

III. A main trunk, largely motor ( = *hyomandibular* less the elements which give rise to the sensory external mandibular), which passes behind the spiracle, all the other branches passing in front of it.

In adult terrestrial Vertebrates (Caducibranchiate Urodeles, Anura, and Amniota) the integumentary sense-organs become reduced, and the corresponding branches of the facial nerve undergo corresponding reduction (Fig. 149); the parts of this nerve which persist are the pharyngeal section (palatine and chorda tympani) and

[1] These branches, together with the lateral line branches of the glossopharyngeal and vagus (p. 187) appear to form an independent and distinct system of *lateral line nerves*, having a common internal origin in the brain, for the innervation of the special sensory organs of the integument in Fishes, Dipnoans and Amphibians. The auditory nerve arises from the same centre.

the main trunk (hyomandibular *less* its lateral line elements). The latter is connected with the glossopharyngeal by the anastomosis of Jacobson, and is distributed, as its name implies, to the region of the first and second visceral arches : thus in Fishes it goes to the parts around the spiracle and to the muscles of the operculum and branchiostegal membrane. A small remnant of this branch in the higher Vertebrates supplies the stylohyoid muscle and the posterior belly of the digastric and the stapedius.

In Mammals the facial is mainly a motor nerve. It is chiefly important in supplying the facial muscles, as well as the platysma myoides, which has the closest relation to them (p. 136). The more highly the facial muscles are differentiated (*e.g.* Primates, especially Homo), the more complicated are the networks formed by the facial nerve.

**Auditory Nerve.**—This large nerve arises in close connection with the facial, and corresponds to a sensory portion of the latter nerve ; [1] it possesses a ganglion (Figs. 148 and 149). Soon after its origin from the brain it divides into a *cochlear* and a *vestibular* branch. The former passes to the lagena or cochlea, while the latter supplies the rest of the auditory labyrinth.

**Vagus group.**—This group includes the **glossopharyngeal, vagus,** and **spinal accessory,** which stand in the closest relation to one another, and are more nearly comparable to the spinal nerves than are the cerebral nerves already described. It consists of both sensory and motor fibres, the former being connected with ganglia (the *jugular* and *petrosal*). The distribution of these nerves differs from that of the other cerebral nerves in not being limited to the head.

Thus the vagus supplies not only the pharynx, tongue, and respiratory organs, but also sends branches to the heart, larynx, and a considerable portion of the digestive tract, as well as to integumentary sense-organs of the trunk in Fishes.

The *spinal accessory* nerve appears for the first time in the Amniota, and will be dealt with after the vagus and glossopharyngeal have been described (p. 187).

The origin of both *glossopharyngeal* and *vagus* by numerous roots in Fishes (Fig. 148) indicates that these nerves correspond to a number of spinal nerves, and this comparison is further justified by the fact that they give off branches in the region of the pharynx and visceral arches, in which a metameric arrangement can be recognised.

In many Fishes and in Dipnoans two or three nerves make their exit from the skull ventrally to the root of the vagus (Fig. 148) : these " spino-occipital "

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[1] On the supposition that the auditory organ corresponds to a modified integumentary sense-organ, the auditory nerve would belong to the lateral line system of nerves (*see* note on p. 185).

or intracranial spinal nerves, which have been described as "ventral roots" of the vagus (*see* p. 143), have nothing to do with this nerve, and perhaps correspond to a part of the hypoglossal of higher Vertebrates.

In Fishes and perennibranchiate Amphibians the glosso-pharyngeal leaves the skull through a special foramen, and not along with the vagus, a *lateral line branch*[1] of which arises separately from and anteriorly to the rest of nerve, dorsally to the glosso-pharyngeal and near the origin of the sensory part of the facial (Fig. 148). This lateral nerve, which may divide into two or even three branches, extends along the side of the body to the tail, either directly beneath the skin, or close to the vertebral column (*c.g.* Elasmobranchii, Dipnoi), and supplies integumentary sense organs.

In Protopterus the vagus also gives off superficial branches which extend along the dorsal, lateral and ventral regions of the body close to the skin. In certain Teleosts (Anacanthini) dorsal and ventral superficial nerves are also present, which have sometimes been described as cutaneous branches of the trigeminal. These require further investigation : they appear to belong mainly to the facial, and from their origin and distribution correspond precisely to the "ramus dorsalis recurrens" of Siluroids. The vagus invariably takes part in their formation, and sometimes also the glossopharyngeal and even the first spinal nerves.

In tracing the development of the lateral nerves, the nervous elements are seen to be so closely united with the thickened epidermis in the region of the lateral line that it is impossible to say whether the nerve arises *in situ* or not; and this is also the case as regards all nerves (VII., IX., X.) supplying integumentary sense organs in the Anamnia.

In branchiate Vertebrates, the glossopharyngeal gives off a pharyngeal branch and forks over the first branchial cleft, while the vagus gives rise to branchial branches which are similarly related to the following clefts (Fig. 148): these branchial nerves supply the muscles and mucous membrane of the branchial apparatus. In Chimæra each of the three branchial nerves arises independently from the brain. It will be remembered that the facial nerve has similar relations to the spiracular cleft (p. 185). Both glossopharyngeal and vagus contain mixed fibres, and become connected in various ways with the trigeminal and facial. In correspondence with the reduction of the gills in higher forms, the branchial branches of the vagus can no longer be recognised, and the glossopharyngeal passes into the tongue as the nerve of taste, giving off also a pharyngeal branch (Fig. 149). This condition is first indicated in Dipnoi and Amphibia.

The *spinal accessory* nerve first appears distinctly in Reptiles. It arises some distance back along the cervical portion of the spinal cord, in the region from which the fourth to fifth cervical nerves come off; from this point it passes forwards as a *collector*, taking up fibres from the cervical nerves as it goes. It extends along the side of the medulla oblongata into the cranial cavity, and

[1] The glossopharyngeal also possesses a lateral line branch in many Fishes.

leaves the skull through the same foramen as the vagus, to which it gives off motor elements. It supplies certain of the muscles related to the pectoral arch, *e.g.* the sternocleidomastoid and the trapezius.

**Hypoglossal.**—The hypoglossal corresponds to one or several of the anterior spinal nerves, and its transformation into a cerebral nerve can be traced in passing through the Vertebrate series. In some Fishes and all Amphibia it does not pass through the cranial wall and is a true spinal nerve ; and in most Fishes and in the Dipnoi, its inclusion within the skull can be seen to be due to a gradual assimilation of the anterior part of the vertebral column with the skull (comp. p. 45). In addition to its numerous ventral-roots one or more dorsal, ganglionated roots have been observed in the embryos of various Vertebrates (Figs. 148 and 149). Two dorsal roots, each with a ganglion, persist in Protopterus, and the same is apparently true as regards Polypterus and certain Elasmobranchs : even amongst Mammals, these roots can exceptionally be recognised subsequently to the embryonic period.[1]

In Fishes (Fig. 148) the hypoglossal, like the next following spinal nerves, sends branches to the muscles of the body, the floor of the mouth, and skin of the back, as well as being connected with the brachial plexus. In higher Vertebrates (Fig. 149) it supplies the intrinsic and extrinsic muscles of the tongue. These *lingual* branches are most marked in Mammals, in which the tongue reaches its highest development. Elements of the cervical spinal nerves also run along with the hypoglossal, and give rise to the so-called *ramus descendens* with which further cervical nerves are associated ; and from the "ansa hypoglossi" thus formed, branches pass to the sterno-hyoid, sternothyroid, omohyoid, and thyrohyoid muscles.

## Sympathetic.

The *sympathetic system* arises in close connection with the spinal system, with which it remains throughout life in close connection by means of *rami communicantes*. It is distributed mainly to the intestinal tract (in the widest sense), the vascular system, and the glandular organs of the body. The sympathetic *ganglia*, like those of the spinal nerves, show originally a segmental arrangement. They usually become united together later by longitudinal commissures and thus give rise to a chain-like paired sympathetic cord lying on either side of the vertebral column. From its ganglia nerves pass off to the above-mentioned

[1] The dorsal root of the first spinal nerve may be reduced or wanting in Mammals — even in Man, so that here the modification of the primary character of the nerves is not limited to those within the skull.

systems of organs, forming numerous plexuses. Peripheral ganglia are also present in the viscera.

The sympathetic extends not only along the vertebral column, but passes anteriorly into the skull, where it comes into relations with a series of the cerebral nerves (comp. pp. 184, 185 and Fig. 149) similar to those which it forms further back with the spinal nerves.

The original segmental character frequently disappears later on and this is especially the case in those regions where marked modifications of the earlier metameric arrangement of the body have taken place—viz., in the neck and certain regions of the trunk, especially towards the tail : thus there are never more than three cervical ganglia in Mammals.

A sympathetic is not known to exist in Amphioxus, and in Petromyzon it appears to be rudimentary. In Fishes proper, it is more highly differentiated, especially in the head region, while in Dipnoans it has not been observed. In Amphibians the sympathetic is well developed, especially in the higher forms (Fig. 121). In the Myctodera it extends anteriorly to the vagus ganglion and posteriorly through the trunk and hæmal canal almost to the apex of the tail, as is the case also in Teleostei.

In the Sauropsida the cervical portion of the sympathetic is usually double, one part running within the vertebrarterial canal alongside the vertebral artery. In all other Vertebrates the whole cord lies along the ventral and lateral region of the vertebral column : it is generally situated close to the latter, and overlies the vertebral ends of the ribs.

## III. SENSORY ORGANS.

The specific elements of the sensory organs originate, like the nervous system in general, from the epiblast ; the peripheral terminations of the sensory nerves are thus always to be found in relation with cells of ectodermic origin, which become secondarily connected by means of nerve-fibres with the central nervous system.

The sensory apparatus was primarily situated on a level with the epidermis and served to receive sensory impressions of but slightly specialised kinds ; but in the course of phylogeny parts of it passed inwards beneath the epidermis, and certain of these became differentiated into organs of a higher physiological order, viz., those connected with *smell, sight, hearing,* and *taste.* These are situated in the head, and except the last mentioned, become enclosed in definite sense-capsules (p. 68) ; they must be distinguished from the simpler *integumentary sense-organs*, which are concerned with the senses of *touch, temperature,* &c.

In many, and more especially in the higher sensory organs,

*supporting* or *isolating cells* can be recognised in addition to the *sensory cells* proper ; both kinds, however, being ectodermic. The mesoderm may also take part in the formation of the sensory organs, giving rise to protective coverings and canals as well as to contractile and nutritive elements (muscles, blood- and lymph-channels).

In the sensory organs of the integument of Fishes as well as in all the higher sensory organs the medium surrounding the end-organ is always moist. In both cases, we meet with *rod-*, *club-*, or *pear-shaped sensory cells*, but in the former the nerves coming from them do not pass through nerve-cells, as they do in the organs of higher sense. This indicates a lower stage of development, there being no differentiation into sensory cell and nerve cell.

In those animals which in the course of development give up an aquatic life and come on land (Amphibia) the external layers of the epidermis dry up, and the integumentary sense-organs pass further inwards from the surface, undergoing at the same time changes of form. Thus from Reptiles onwards the rod-shaped end-cell no longer occurs, and two kinds of nerve-endings are seen in the skin —*terminal cells*, and fine intercellular nerve-networks known as *free nerve-endings.*

## Sense-Organs of the Integument.

### *a. Nerve-eminences.*

In Amphioxus certain rod-shaped or pear-shaped cells can be recognised in the epidermis, especially in the anterior part of the animal ; each of these is provided distally with a hair-like process and proximally is in contact with a nerve. The cells are distributed irregularly, but in the neighbourhood of the mouth and cirri they tend to form groups.

It is doubtful whether these structures in Amphioxus are directly comparable to the integumentary sense-organs of Fishes and Amphibians, but it is important to note that each of the latter always arises in the first instance from a single cell which forms a group by division. These organs always consist of *central* cells, arranged in the form of a rounded and depressed pyramid, and of a *peripheral* mass grouped around the former like a mantle. The central cells are surrounded by a network of nerve-fibres ; each of them bears at its free end a stiff cuticular hair, and they are to be looked upon as the sensory cells proper. The others function only as a supporting and slime-secreting mass (Figs 150 and 151).

In Dipnoi, aquatic Amphibia and all amphibian larvæ these organs retain throughout life their peripheral free position, on

a level with the epidermis,[1] but in Fishes they may in post-embryonic time become enclosed in depressions or complete canals,[2] which are formed either by the epidermis only, or, as is more usually the case, by the scales and bones of the head, and which open externally. The organs are thus protected.

These sensory organs are situated characteristically along certain tracts, the position of which is very constant: in the head, *supra-orbital, infra-orbital,* and *hyomandibular* tracts can be recognised, and a *lateral line* (or several— Proteus and all Amphibian larvæ) extends along the sides of the body to the caudal fin (Figs. 152 and 153). They are thus often spoken of as *segmental sensory organs* or *organs of the lateral line*.[3] The portions lying in the region of the head are innervated by the lateral

FIG. 150.—TRANSVERSE SECTION OF A FREELY PROJECTING SEGMENTAL SENSE-ORGAN.

The cuticular tube and the surrounding epidermic cells are not represented, *CZ*, central (sensory) cells; *MZ*, *MZ*[1], peripheral cells.

line branches of the facial, glossopharyngeal, and vagus (*see* note on p. 185).

Freely projecting nerve-eminences are not present in Rays and Ganoids, and are only of minor importance in Sharks. In all these Fishes the integumentary sense-organs are more or less deeply situated, being enclosed in complete or incomplete canals arising as proliferations of the epidermis extending into the dermis, and becoming greatly branched.

The so-called *Savi's vesicles* of Torpedo, the "*nerve sacs*" of Ganoids, and the *ampullæ* of Elasmobranchs, correspond to modified nerve-eminences. They are all limited in their distribution to the head and anterior portion of the trunk, being most numerous on the snout: they arise from thickenings of the epidermis which later become invaginated and in which a sensory epithelium is differentiated. In Ganoids these organs retain a simple sac-like form, and in Torpedo they become completely separated off from the epidermis, while in other Elasmobranchs they are tubular, each tube giving rise to one or more swellings or ampullæ, separated

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[1] At the time when an Amphibian undergoes metamorphosis and gives up its aquatic habits, these sensory organs sink downwards into the deeper layer of the skin, and, as the epidermis grows together over them, they become shut off from the exterior and reduced, and may finally disappear. (Anura and certain Caducibranchiata.) In other Urodeles they may, in some cases, be retained throughout life, and are said to come to the surface when the animal returns to tne water during the breeding season; but, more usually, new organs then become developed.

[2] This is also the case on the head in Dipnoans.

[3] In the Dipnoi they are not limited to the lateral line, and in Marsipobranchii they have no regular arrangement and are not numerous, although a lateral branch of the vagus is present.
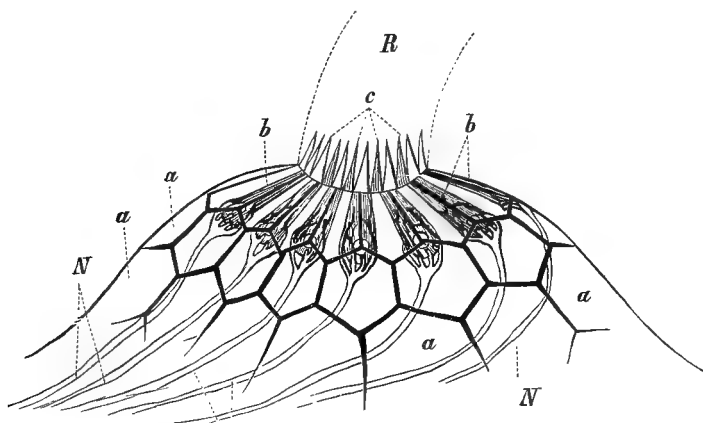
Fig. 151.—Nerve Elevation of a Urodele.   (Semidiagrammatic.)

$a$, $a$, cells of the epidermis, through which the neuro-epithelium, $b$, $b$, can be
seen ; $c$, the terminal hairs of the latter (the peripheral cells are not repre-
sented) ; $R$, hyaline tube, formed as a secretion ; $N$, the nerve-fibres passing
to and surrounding the sensory cells.
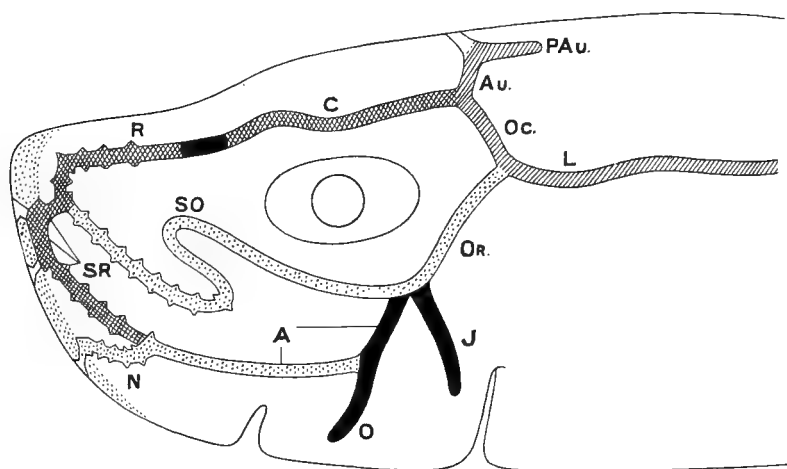


Fig. 152.—Sensory Canals of *Chimæra monstrosa*.   (After F. J. Cole.)   The
innervation is indicated by the different kinds of shading.

(1.) Supra-orbital canal (innervated by superficial ophthalmic of facial—cross-
hatched—the black segment is the portion innervated by the profundus) =
cranial $(C)$ + rostral $(R)$ + sub-rostral $(SR)$.

(2.) Infra-orbital canal (buccal + otic of facial—dotted) = orbital $(Or)$ + sub-
orbital $(SO)$ + portion of angular $(A)$ + nasal $(N.)$

(3.) Hyomandibular or operculo-mandibular canal (external mandibular of facial
—black) = remainder of angular $(A)$ + oral $(O)$ + jugular $(J.)$

(4.) Lateral canal (lateral line branch of vagus—oblique shading) = lateral $(L)$ +
occipital $(Oc)$ + aural $(Au)$ + post-aural $(PAu.)$

off from the rest of the tube by radial folds of connective tissue, and containing the nerve-endings. The tubes are filled with a gelatinous substance.

The function of the nerve eminences is doubtful, but it appears that they are concerned with the perception of mechanical stimuli
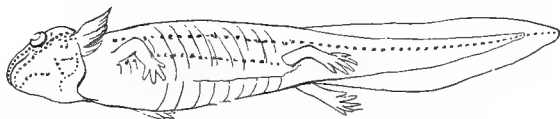


FIG. 153.—DISTRIBUTION OF THE LATERAL SENSE-ORGANS IN A SALAMANDER LARVA.

from the surrounding water, and thus are important as regards the appreciation of the direction of these stimuli.

The horny wart-like structures arising periodically during the breeding season in Cyprinoids and known as "pearl organs," are due to a modification of the reduced nerve-eminences. Similar structures occur in Anura.

### b. End-buds.

The nerve eminences pass through a stage in development in which they clearly resemble end-buds, and the latter may be looked upon as the phyletically older organs, which do not become so highly differentiated as the former. No sharp line of demarcation can, however, be drawn between the two, as all kinds of intermediate forms are met with : they are here described separately merely for the sake of clearness.

In contrast to the nerve-eminences, which tend to sink below the surface, the end-buds usually form a dome-like elevation projecting above the general level of the epidermis. A central sensory epithelium, provided with sensory hairs, and peripheral supporting cells can be recognised, but the former are as long as the latter.

In Lampreys and most Elasmobranchs they remain at a primitive stage of development, but become of great importance in Ganoids and Teleosts, in which they are scattered irregularly over the whole body and are particularly numerous in the fins, lip-folds, barbules, and mouth. From the Dipnoi onwards they become limited to the oral and nasal cavities. In Dipnoi and Amphibia they occur on the papillæ of the oral and pharyngeal mucous membrane and tongue. In Reptiles their distribution is somewhat more limited, and this is still further the case in Mammals, in which, however, they are still found on the soft palate, on the walls of the pharynx, and even extend into the larynx ; but here they are most numerous on the tongue, where they occur, situated more deeply, on the circumvallate and fungiform papillæ as well as on the papilla foliata, and function as *organs of taste*.

O
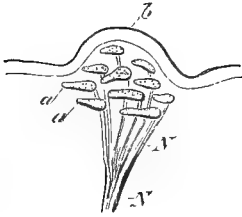
FIG. 154A.—A TACTILE SPOT FROM THE SKIN OF THE FROG. Semi-diagrammatic. (Modified from Merkel.)

$N$, nerve, which loses its medullary sheath at $N^1$; $a$, $a$, neuro-epithelium; $b$, epidermis.
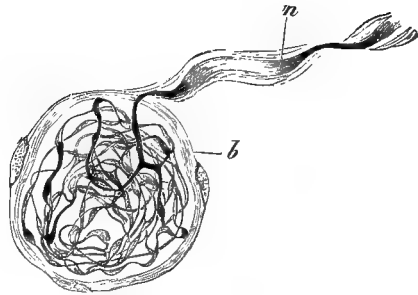
FIG. 154C.—A TACTILE CORPUSCLE (END-BULB) FROM THE MARGIN OF THE CONJUNCTIVA OF MAN. (After Dogiel.)

$n$, medullated nerve fibre, the axis-fibre of which passes into a closely coiled terminal skein; $b$, nucleated fibrous investment.
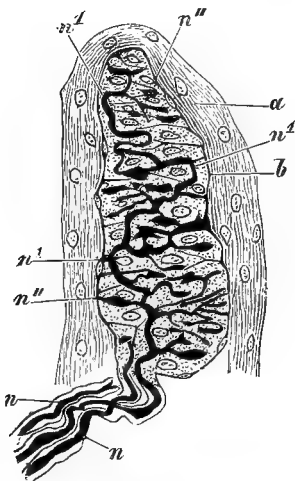
FIG. 154B.—DERMAL PAPILLA FROM THE HUMAN FINGER ENCLOSING A TACTILE CORPUSCLE. (After Lawdowski.)

$a$, fibrous and cellular investment; $b$, tactile corpuscle, with its cells; $n$, nerve-fibre; $n'$, the further course of the nerve-fibre, showing its curves and bends; $n''$, terminal twigs of the nerve-fibres with club-shaped endings.
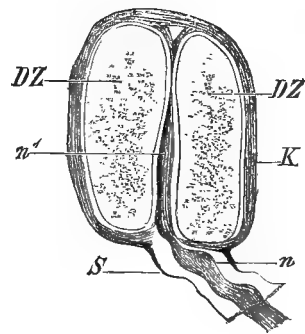
FIG. 154D.—TRANSVERSE SECTION THROUGH A TACTILE CORPUSCLE FROM THE BEAK OF A DUCK. (After Carrière.)

$n$, nerve, entering the capsule $K$, its sheath ($S$) becoming continuous with the latter. The nerve passes between the two covering-cells, $DZ$, $DZ$, widening out to form a tactile plate at $n^1$.

### c. *Tactile-cells and corpuscles.*

(Terminal ganglion cells.)

In these structures there is no longer any direct connection with the surface of the epidermis, and supporting cells are wanting.

" Tactile spots," consisting of groups of *touch cells*, are met with for the first time in tailless Amphibians, in which they are situated mainly on small elevations, and are distributed over the skin of the whole body (Fig. 154A).    In Reptiles they are found chiefly in the region of the head, on the lips and sides of the face, and on the snout, but in some cases (as in Blindworms and Geckos), they extend over the whole body close to the scales.    In Snakes and Birds the tactile cells are confined to the mouth-cavity (tongue) and to the beak (cere), and lie much more closely together, forming definite masses, or tactile corpuscles (Fig. 154D). Each of these is surrounded by a nucleated connective-tissue investment, from which septa extend into the interior, partially separating the individual tactile cells from one another.    In Mammals the tactile cells are either isolated—as, for instance, on the hairless portions of the body, or they give rise to oval corpuscles, each consisting of a many-layered and nucleated investment, into which a nerve passes, becomes twisted up, and comes into relation with one or more terminal cells (Fig. 154 B, C).    These are most numerous and highly developed on the volar and plantar surfaces of the hand and foot respectively, and on the conjunctiva and snout.

### d.    *Club-shaped corpuscles.*

(Pacinian corpuscles.)

From the Reptilia (Lizards, Snakes) onwards, club-shaped corpuscles are present in addition to the above-described tactile-organs.    In these Reptiles they occur chiefly in the region of the lips and teeth ; they have an elongated, oval form, and their structure is simple.

In the interior of each corpuscle is seen the continuation of the axis-fibre of the nerve which becomes swollen distally, and externally to this is a double column of cells which enclose the club-shaped axis (Fig. 155).    It is probable that a fine branch is given off from the axis-fibre to each cell.    The column of cells is enclosed externally by an investment consisting of numerous nucleated lamellæ in which longitudinal and circular layers can be distinguished.

Organs of this kind are universally present, deeply situated,

in the skin of Birds and Mammals, and in the former they are
particularly abundant on the beak and at the bases of the con-
tour-feathers of the wings and tail,
and are also found on the tongue.
They occur, moreover, in various
other regions, both in Birds and
Mammals (*e.g.* the various organs
of the abdominal cavity, the con-
junctiva, the fasciæ, tendons, liga-
ments, vas deferens, periosteum, peri-
cardium, pleura, corpus cavernosum
and spongiosum, the wing-membrane
of Bats, &c.).

The tactile cells and tactile and
club-shaped corpuscles are all con-
cerned with the sense of *touch*. It
is impossible to say definitely what
nerve-endings have to do with the
perception of *temperature;* it is not
improbable that the touch cells, as
well as the nerve-fibres often pro-
vided with varicose swellings which
end freely in the epidermis, are con-
cerned in this process. Such *free
nerve-endings* occur in the skin of
all Vertebrates, and consist of an
intercellular network, no direct con-
nection between nerve and epithelial
cell having been observed.



Fig. 155. —A Pacinian Cor-
puscle.

*A*, axis fibre; *A*[1], tufted or knob-
like end of the same ; *NS*, nuc-
leated sheath of nerve, which
passes into the external longi-
tudinal series of lamellæ, *L* ; *Q*,
internal, circular layer of the
external part of the club ; *JK*,
internal part of the club formed
of the cell-pillars.

### OLFACTORY ORGAN.

The olfactory lobe as already mentioned (p. 153) represents a pro-
longation of the secondary fore-brain, the ventricle of which is tem-
porarily or permanently continued into it.    In some cases it becomes
differentiated into olfactory bulb, tract, and tubercle (pp. 159–175).

The olfactory *nerves* proper are connected with the bulb, and are
usually arranged in a single bundle on either side, with more or less
distinct indications of a subdivision into two bundles : they ap-
parently arise in continuity with the epithelium of the nasal
involution (comp. pp. 177, 187) and then grow centripetally,
uniting with the olfactory lobe or bulb secondarily.

In all Mammals but Ornithorhynchus, as well as in Menopoma,
Apteryx, and the extinct Dinornis, the olfactory nerves pass into
this nasal cavity separately, through a cribriform plate of the
ethmoid (p. 99).

The primary origin of the olfactory organs is by no means understood : possibly it may have arisen by a modification of primitive integumentary sense-organs. It is doubtful whether the organ can be said to have a true olfactory function in Fishes and perennibranchiate Amphibians.

In its simplest form, the olfactory organ consists of a ventral, paired, pit-like depression of the integument of the snout opening on to the surface by an external nostril. It is lined by an epithelium which is connected with the brain by the olfactory nerves. The olfactory mucous membrane contains sensory cells, or olfactory cells proper—usually provided with sensory hairs, separated by isolating or supporting cells, both kinds having a smilar origin (Fig. 156).

These olfactory cells are said to constitute the only true *neuro-epithelium* in Vertebrates, as the nerve arises in connection with the cell itself, with which it remains continuous, as in many Invertebrates (*primary sensory cell*, Retzius). The cell is therefore not merely surrounded by a nerve-network as in other *secondary* nerve-cells, and the olfactory organ thus probably represents a very ancient structure phylogenetically. It is possible, however, that the central cells of the integumentary sense-organs of Anamnia (*e.g.* end-buds) may be directly continuous with their nerves, although surrounded by a nerve-network.



FIG. 156. — EPITHELIUM OF THE OLFACTORY MUCOUS MEMBRANE. A, of *Petromyzon planeri*; B, of *Salamandra atra*.

R, olfactory cells ; E, interstitial epithelial cells.

From the Amphibia onwards glandular elements are present, the secretion of which serves to keep the nasal cavity moist.

The olfactory organs of all the true Fishes exhibit the above-described simple sac-like form, but from the Dipnoi onwards they come to communicate with the cavity of the mouth as well as with the exterior. In consequence of this, *anterior* or *external*, and *posterior* or *internal nostrils (choanæ)* can be distinguished, and as a free passage is thus formed through which air can pass, the olfactory organ takes on an important relation to the respiratory apparatus.

In **Amphioxus**, the ciliated pit situated above the anterior end of the central nervous system probably represents an unpaired olfactory organ. Traces of a structure possibly homologous with this are said to occur in the embryos of the Lamprey and Sturgeon.

**Cyclostomes.**—In these forms (Fig. 54) the olfactory organ consists of a sac, containing numerous radial folds of the mucous membrane, and *unpaired* externally. It lies close in front of the cranial cavity, and opens on the *dorsal* surface of the anterior part of the head by a longer or shorter chimney-like tube. In

Myxine this tube is long, and is supported by rings of cartilage. In the larval lamprey the organ is at first ventral and unpaired (Fig. 125), but subsequently becomes sunk in a common pit with the pituitary invagination and takes on a dorsal position : it is almost completely divided into two lateral halves internally by the formation of a fold of the mucous membrane. The pituitary sac thus extends backwards from the ventral side of the organ above the mucous membrane of the mouth : in Petromyzon it ends blindly, but in Myxine it opens into the oral cavity, perforating the skull floor from above instead of from below as in other Vertebrates.

**Fishes.**—The position of the olfactory organ in Elasmobranchs (Fig. 157, A) differs from that seen in Cyclostomes in lying on the
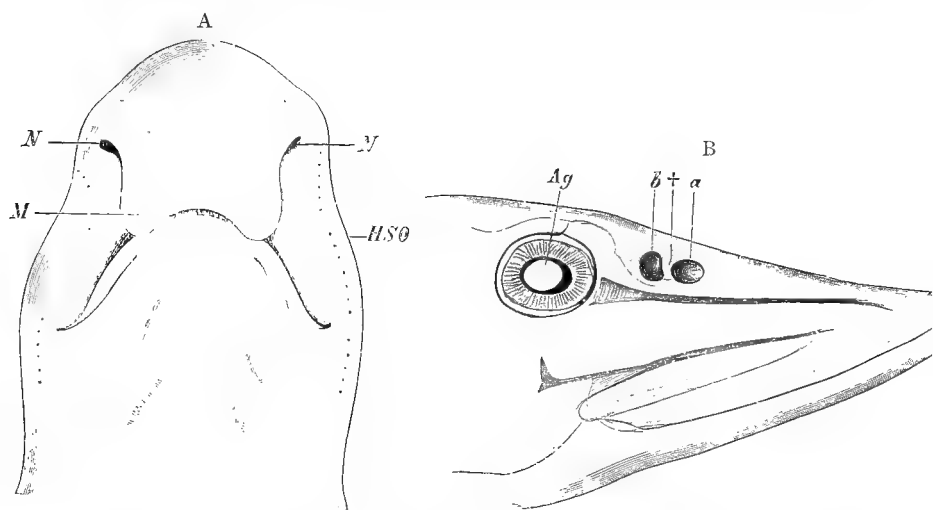


Fig. 157.—*A*, Ventral View of the Head of a Dogfish (*Scyllium canicula*). *N*, external nostril ; *M*, mouth ; *HSO*, integumentary sense-organs.

*B*, Lateral View of the Head of a Pike (*Esox lucius*). *a* and *b*, the anterior and posterior openings of the external nostrils ; †, fold of skin separating *a* and *b* ; *Ag*, eye.

under instead of the upper surface of the snout, and thus retains the more primitive position. From these Fishes onwards the organ is always *paired*, each sac being more or less completely enclosed by a cartilaginous or bony investment forming an outwork of the skull.

From the Ganoids onwards it always has a similar position with regard to the skull, being situated between the eye and the end of the snout, either laterally or more or less dorsally : originally, however, it is ventral. In the course of development each external nostril of Ganoids and Teleosts becomes completely divided into

two portions, an anterior and a posterior (Figs. 157, B, and 158), by
a fold of skin. The nostril often lies at the summit of a longer or
shorter tube, lined with ciliated cells, and the distance between
the anterior and the posterior aperture varies greatly, according to
the width of the fold of skin which separates them.

The mucous membrane of the nasal organ of Fishes is always
raised up into a more or less complicated system of folds, which
may have a transverse, radial, rosette-like, or longitudinal arrange-
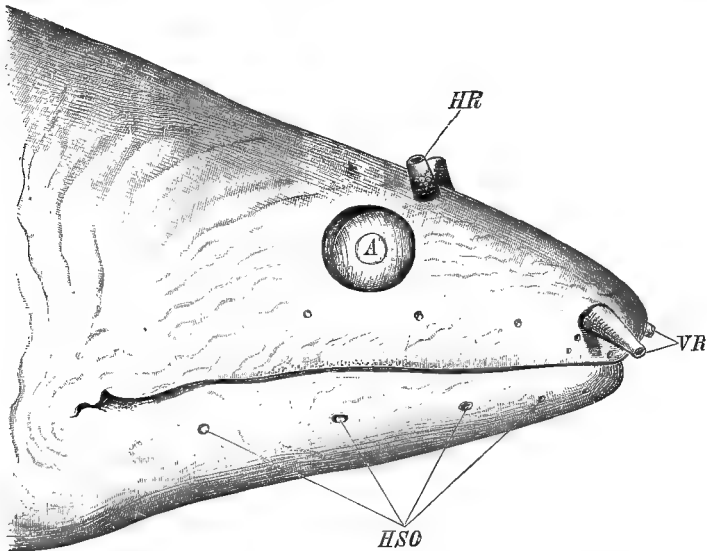


FIG. 158.—LATERAL VIEW OF THE HEAD OF *Muræna helena*.

*VR* and *HR*, anterior and posterior tubes of the external nostrils ; *A*, eye ;
*HSO*, integumentary sense-organs.

ment, and which are supplied by the branches of the olfactory
nerve.

The olfactory organ of Polypterus is more highly developed and compli-
cated than that of any other Fish. In certain representatives of the Plecto-
gnathi and Gymnodontes amongst the Teleostei, on the other hand, the organ
shows various stages of degeneration.

**Dipnoi.**—A nasal skeleton well differentiated from the skull
proper is met with for the first time in Dipnoans. In Protopterus
it consists of a cartilaginous trellis-work enclosing each olfactory
sac and united with its fellow in the median line by a solid septum :
the floor is formed mainly by the pterygopalatine and by con-
nective tissue. The mucous membrane is raised into numerous
transverse folds connected with a longitudinal fold, and the olfac-
tory organ in general most nearly resembles that of Elasmobranchs,

except that, as already mentioned, *posterior (internal)* as well as anterior (external) nostrils are present. The latter open beneath the upper lip, and so cannot be seen when the mouth is closed; the former open into the oral cavity rather further back.

The peculiar position of the anterior nares has a physiological significance, at any rate in Protopterus, in connection with its habits (see p. 17); during its summer sleep the animal breathes through a tube, passing between the lips, formed from the capsule or cocoon which encloses it. The necessary moisture for the olfactory mucous membrane during this time is provided by the numerous goblet cells which line the walls of both nostrils.

**Amphibia.**—The olfactory organ of the Perennibranchiata resembles in many respects that of the Dipnoi: it is always enclosed within a complete or perforated cartilaginous capsule situated laterally to the snout close beneath the skin, and is not protected by the bones of the skull (Fig. 159). Its floor is largely fibrous, and the mucous membrane is raised into radial folds like those of Cyclostomes and Polypterus. In all the other Amphibia it becomes included within the cranial skeleton, and lies directly in the longitudinal axis of the skull in front of the cranial cavity.



FIG. 159.—OLFACTORY ORGAN OF *Necturus maculatus.* (From the dorsal side.)

*N*, olfactory sac; *Ol*, olfactory nerve; *Pmx*, premaxilla; *F*, frontal; *P*, process of the parietal; *PP*, palato-pterygoid; *AF*, antorbital process.

The structure of the olfactory organ now becomes modified in correspondence with the change in the mode of respiration; the nasal chamber becomes differentiated into an *olfactory* and a *respiratory portion*, and an extension of the olfactory surface takes place by the formation of one or more prominences on the floor and side-walls of the nasal cavity. These prominences, which may be compared to the *turbinals* of higher forms, are present in certain Myctodera (Fig. 160), and attain a very considerable development in Anura and Gymnophiona, especially in the latter, in which the nasal chamber is converted into a complicated system of spaces and cavities. A *main* chamber and a more laterally situated *accessory* cavity can in all cases be distinguished, even in the Derotremata and Myctodera; the accessory cavity lies in the maxillary bone (Fig. 160 and 165 A—E).

In certain Gymnophiona the accessory chamber becomes entirely shut off from the main cavity and receives a special branch of the olfactory nerve, so that in these cases two separate nasal cavities can be distinguished.

*Glands*, situated under the olfactory mucous membrane, are now also met with; these are either diffused, or united to form definite masses.   They either open directly into the nasal cavity, their secretion serving for the necessary moistening of the mucous membrane (effected in Fishes by the external medium), or they pour their secretion into the pharynx or posterior nostrils.   The latter always lie tolerably far forwards on the palate, and are for the most part enclosed by the vomer, as well as the palatine.

Finally, the *naso-lachrymal duct* must be mentioned : it passes out from the anterior angle of the orbit, through the lateral wall
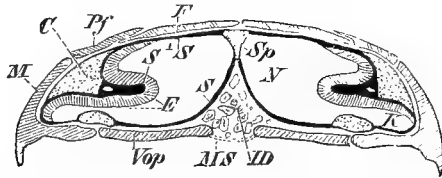


Fig. 160.—Transverse Section through the Olfactory Cavities of *Plethedon glutinosus* (Myctodera).

*S, S,* olfactory mucous membrane ; *N,* main nasal cavity ; *K,* maxillary cavity ; *C,* cartilaginous, and *S¹*, fibrous portion of the turbinal, which causes the olfactory epithelium (*E*) to project far into the nasal cavity ; *ID,* intermaxillary gland, shut off from the cavity of the mouth by the oral mucous membrane (*MS*) ; *F*, frontal ; *Pf*, prefrontal ; *M*, maxilla ; *Vop,* vomeropalatine ; *Sp,* nasal septum.

of the nose, and opens into the nasal cavity on the side of the upper jaw.   It conducts the lachrymal secretion from the conjunctival sac of the eye into the nasal cavity, and arises in all Vertebrates, from the Myctodera onwards, as an epithelial cord which is separated off from the epidermis, and, growing down into the dermis, becomes hollow secondarily.

**Reptilia.**—Owing to the growth of the brain and facial region and to the formation of a secondary palate (p. 92), the olfactory organs, from Reptiles onwards, gradually come to be situated more ventrally, beneath the cranium.

The Lacertilia, Ophidia, and many Chelonia possess the simplest olfactory organs amongst Reptiles.   The nasal cavity of Lizards is divided into two portions, a smaller outer (anterior), and a larger inner (posterior)—or olfactory chamber proper.   The latter only is provided with sensory cells, the former being lined by ordinary stratified epithelium continuous with the epidermis and containing no glands.   A large turbinal, slightly rolled on itself, arises from the outer wall of the inner nasal chamber, and extends far into its lumen ; this is also well developed in Ophidia, in which a distinct outer nasal chamber is wanting ; it may be derived from that of the Amphibia.

A large gland which opens at the boundary between the inner and outer nasal cavities lies within the turbinal. Below the latter is the aperture of the lachrymal duct : this duct in some Reptiles opens on the roof of the pharynx (Ascalabota), and in others into the internal nostrils (Ophidia).

The structure of the nose in Chelonians is very complicated and varied. In marine Chelonians it is divided into two passages, one above the other, and connected by means of a perforation of the septum. The comparative paucity of glands in the olfactory organ of Lizards and Snakes forms a marked contrast to the condition seen in Chelonians, the nasal organ of which is characterised by a great abundance of them.
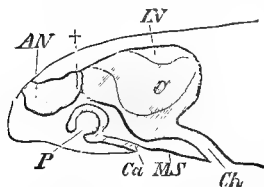


FIG. 161.—DIAGRAM OF THE OLFACTORY ORGAN OF A LIZARD. (Longitudinal vertical section.)

*AN*, *IN*, outer and inner nasal chambers ; +, tube-like connection between them ; *Ch*, internal nostrils ; *P*, papilla of Jacobson's organ ; *Ca*, aperture of communication of the latter with the mouth ; *MS*, oral mucous membrane.

The extension downwards and backwards of the olfactory organ is most marked in Crocodiles, in correspondence with the growth forwards of the facial region and the formation of the palate ; its posterior part thus comes to lie below the brain and base of the skull. Each nasal chamber is divided posteriorly into two superimposed cavities, the upper of which represents the proper olfactory chamber, and is lined by sensory epithelium, while the lower functions as a respiratory portion only. Certain accessory air-chambers are connected with the nasal cavity. A large gland is present between the olfactory chamber and its investing bones, and opens into the nasal cavity. As in other Reptiles, there is only a single true turbinal, but externally to it lies a second prominence, which may be spoken of as a *pseudo-turbinal*.

**Birds.**—In all Birds, as in Lizards, there is an outer chamber, lined by stratified epithelium, and a proper olfactory chamber, situated above the former. Birds also possess only a single true turbinal—if by this term is understood a free independent projection into the nasal cavity supported by skeletal parts. Two other prominences (pseudo-turbinals) are, however, present ; one of which lies, like the true turbinal, in the proper olfactory chamber, while the other, like the pseudo-turbinal of the Crocodile, is situated in the outer portion : these are simply incurved portions of the whole nasal wall (Fig. 162).

The form of the true turbinal, which is usually supported by cartilage—more rarely by bone, varies greatly. It is either represented by a moderate-sized prominence, or else it becomes more or less rolled on itself. The lachrymal duct opens below and an-

teriorly to it. This turbinal is comparable to that of Urodeles and Reptiles.

The so-called external nasal gland of Birds is situated on the frontal or nasal bones, along the upper margin of the orbit. It is supplied by the first and second branches of the trigeminal, and corresponds to the lateral nasal gland of Lizards.

**Mammals.**—Corresponding to the much more marked development of the facial portion of the skull, the nasal cavity of Mammals is proportionately much larger than in the forms yet described, and consequently there is much more room for the extension of the turbinals: these give rise to a spongy labyrinth, the cell-like compartments of which are lined by mucous membrane ; and thus variously shaped projections, supported partly by cartilage and partly by bone, are seen extending into the nasal cavity (Fig. 163, A–C).

The normal number of these true *olfactory ridges* or *scrolls* varies considerably.[1] They may be arranged in one row (Ornithorhynchus, Cetacea, Pinnipedia, Primates), or in several rows (other Mammals), in which latter case the olfactory lobes are largely developed.

FIG. 162.—TRANSVERSE SECTION THROUGH THE RIGHT NASAL CAVITY OF A SHRIKE (*Lanius minor.*)

*O.M*, *M.M*, superior (pseudo) and middle (true) turbinal ; *a*, upper, and *b*, lower nasal passage ; *LR*, air-chamber, which extends into a hollow of the superior turbinal.

According to the degree of development of the olfactory apparatus, taking specially into account its cerebral portion (olfactory lobes), we may distinguish between Mammals which are *macrosmatic* (the majority of the mammalian orders), *microsmatic* (Seals, Whalebone Whales, Monkeys, Man), and *anosmatic* (most Toothed Whales).

The above-mentioned olfactory scrolls belong to the true olfactory region, and are generally described as "*ethmoid turbinals*," as in all but the first of the series their skeletal supports usually become united with the ethmoid bone, the first coming into relation with the nasal, and being therefore usually spoken of as the "*nasal turbinal.*" It must, however, be borne in mind that these do not correspond to the turbinals of lower Vertebrates. The latter are represented by the so-called "*maxillary turbinal*," situated in the anterior (lower) portion of each nasal chamber, which communicates with the pharynx by the internal nostrils, its skeletal portion becoming united with the maxillary bone (Fig. 163, C). This maxillary turbinal no longer possesses an olfactory epithelium

[1] In most of the Mammalian orders, five olfactory scrolls are typically present ; in Echidna there are six or more ; in Ungulates there may be as many as eight ; amongst Edentates, Orycteropus possesses eleven ; while in adult Primates there are only from one to three, a greater number being present in the embryo (Fig. 163).

after the embryonic period,[1] and has plainly undergone a change of function in connection with the perception of the warmth and moisture of the inspired air. When well developed, it forms a single or double coil, and may even be more or less branched (Fig. 164). Branches of the trigeminal extend over it, and supply its mucous membrane. An olfactory and a respiratory region can therefore also be distinguished in the nasal chamber of Mammals.



Fig. 163, A.—Lateral View of the Nasal Chamber of a Human Embryo.

*I, II, III*, the three olfactory ridges ; †, supernumerary ridge which occurs in the embryo; *n*, tip of the nose ; *pl*, hard palate ; *cr*, base of skull ; *os*, Eustachian aperture.

nasal apparatus, but may lose their primary function, often persisting merely as air-sinuses.

The nasal glands may be divided into two sets, —numerous small, diffuse *Bowman's* glands, and a large *gland of Stenson*. The latter appears early in the embryo, and often becomes greatly reduced later on in development; it is situated in the lateral or basal walls of the nasal cavity, and may extend into the maxillary sinus when the latter is well developed.

The appearance of an *external nose* is very characteristic of the olfactory organ of Mammals : this must be regarded as a derivative of the outer chamber of the nose of Reptiles and Birds.

The nasal chamber usually communicates with neighbouring cavities, such as the maxillary, frontal, and sphenoidal sinuses (Fig. 163, B, C) : the two last-mentioned cavities arise in connection with the



Fig. 163, B.—Sagittal Section through the Nasal and Buccal Cavities of the Human Head.

*I, II, III*, the three olfactory ridges ; *sn'*, frontal sinus ; *sn''*, sphenoidal sinus ; *os*, aperture of Eustachian tube ; *bc*, entrance to the mouth ; *lg*, tongue ; *v.i*, atlas vertebra ; *v.ii*, axis vertebra.

[1] This is also true of the anterior (lower) ethmoid turbinal in microsmatic Mammals.

It is supported by an outward extension of the nasal bones and by the cartilaginous septum nasi which arises from the ethmoid, as well as by other secondarily independent cartilages (*ali-nasals*) which were primarily continuous with the general cartilaginous wall, but become differentiated from the latter in various ways in accordance with the varied functional adaptations which the outer nose undergoes. Thus it may be provided with a special valvular apparatus for closing the nostrils (aquatic Mammals); or may grow out to form a longer or shorter trunk provided with a complicated musculature (Mole, Shrew, Pig, Tapir, Elephant), and, by means of its abundant nerve-supply, serve as a delicate organ of touch and even as a prehensile apparatus.
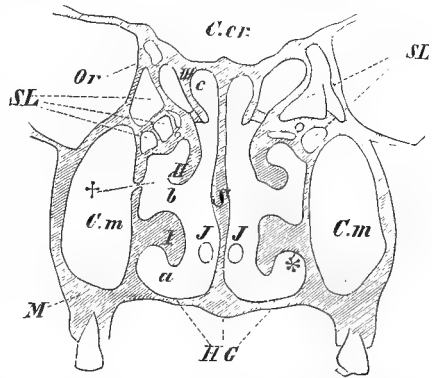


FIG. 163, C.—TRANSVERSE VERTICAL SECTION THROUGH THE NASAL CAVITY OF MAN.

*I, II, III*, inferior (maxillary), middle, and superior turbinal; *a, b, c*, inferior, middle, and superior nasal passage; *S*, septum nasi; *J, J*, position of rudimentary Jacobson's organs, which are situated nearer the floor of the cavity than is indicated in the figure; *\**, point at which the naso-lachrymal duct opens; *†*, entrance into the maxillary sinus (*C.m*); *SL*, ethmoidal labyrinth; *HG*, hard palate; *C.cr*, cranial cavity; *M*, maxilla; *Or*, wall of orbit.
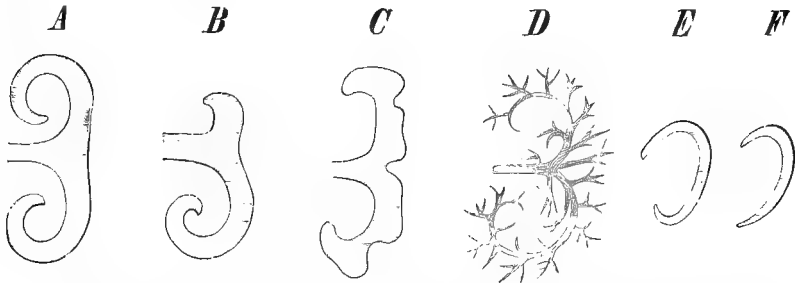


FIG. 164.—VARIOUS FORMS OF THE MAXILLO-TURBINAL OF MAMMALS.

*A*, double coil; *B*, transition from latter to single coil, *E, F*; *C*, transition from double coil to the dendritic form D.    (After Zuckerkandl.)

## JACOBSON'S ORGAN.

By the term " Jacobson's organ " is understood a paired accessory nasal cavity which in an early embryonic stage becomes differentiated from the nasal chamber, and which is supplied by the olfactory and trigeminal nerves; it communicates with the mouth by a special aperture.
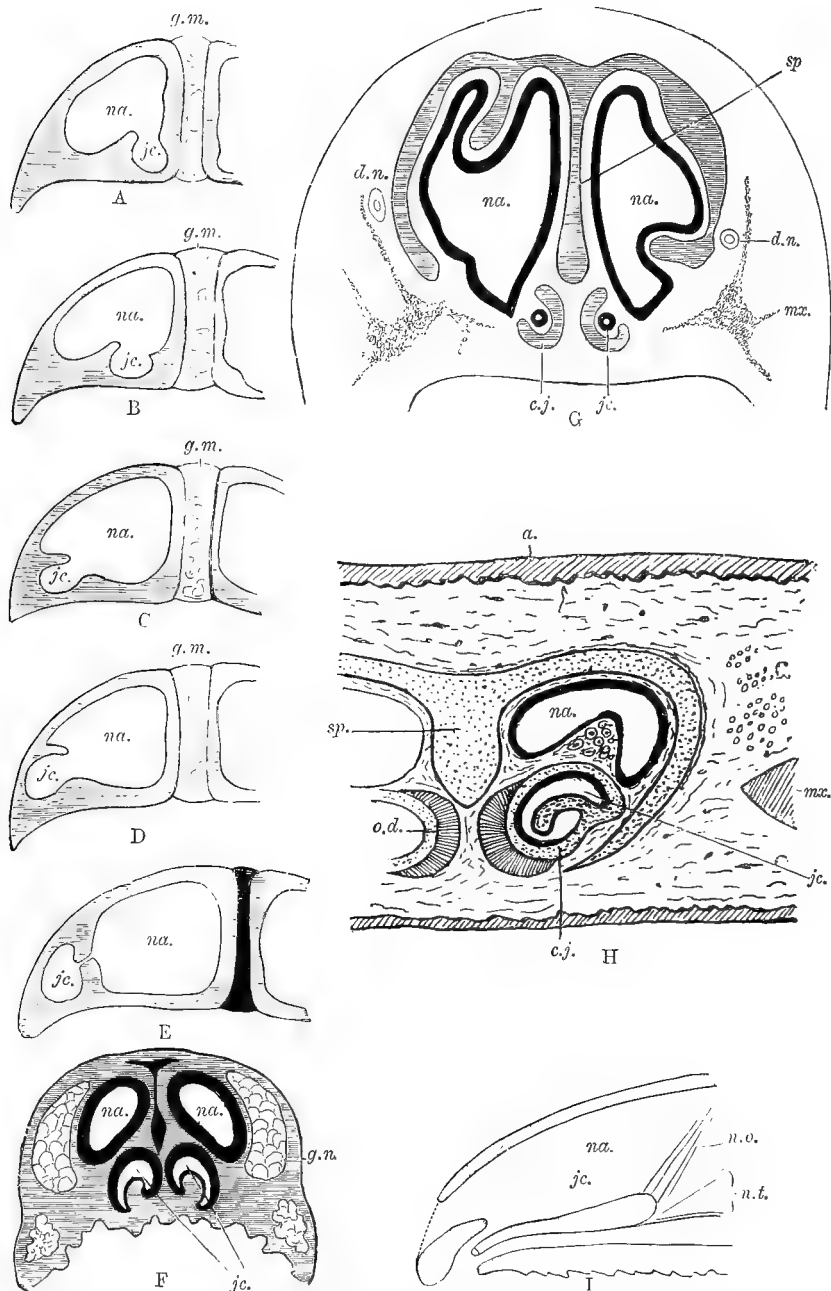
FIG. 165.—TRANSVERSE SECTIONS OF THE NOSE IN VARIOUS VERTEBRATES.

A—D, Illustrating the various ontogenetic and phylogenetic stages of the Jacobson's organ of Urodeles. In A its position is median, and in D lateral.

E, Gymnophiona, in which the organ becomes separated from the main nasal cavity.

F, Lacerta agilis.

G, Placental Mammal; I, the same, in longitudinal vertical section.

H, Ornithorhynchus. (After Symington.)

N, main nasal cavity; jc, Jacobson's organ; c.j, Jacobson's cartilage; g.m, intermaxillary gland; g.n, nasal gland; n.o, olfactory nerve; n.t, trigeminal nerve; d.n, naso-lachrymal duct; mx, maxilla; o.d, dumb-bell shaped bone.

A Jacobson's organ is first met with in Amphibians. In young Triton larvæ a small gutter-like medio-ventral outgrowth of each nasal cavity arises, with which the ventral branch of the olfactory nerve comes into relation. This outgrowth later undergoes a relative change of position, and comes to be situated laterally towards the upper jaw (Fig. 165 A–D). At its blind end a gland is developed. In Siren the primary median position is retained, and in the Axolotl it does not extend so far laterally as in the adult Triton. The accessory nasal chamber of Cœcilians [1] (p. 200) is developed in a similar manner (E), and a large gland is in connection with it. There can also be little doubt that this cavity is represented in Anura, although its relative position is somewhat different to that seen in Urodeles.

The Jacobson's organ of the Amniota is also developed in the medio-ventral part of the nasal chamber, close to the septum nasi. It loses its primary connection with the former, but retains its median position, lying between the floor of the nasal cavity and the roof of the mouth. It is lined by an olfactory epithelium and communicates in front with the mouth through the corresponding naso-palatine canal (p. 100). In Lacertilia and Ophidia a papilla extends into its cavity from the floor (Figs. 161 and 165, F).

These organs are not present in Crocodiles, Chelonians, and Birds, but rudiments have been observed in embryos of Crocodilus biporcatus, and certain cartilages on the nasal floor in Birds appear to correspond with the Jacobson's cartilages of other forms.

Amongst Mammals, Jacobson's organ is most marked in Monotremes (Fig. 165, H), in which it is much more highly developed than in Lizards. It contains a well-marked, turbinal-like ridge, supported by cartilage continuous with that enveloping the organ and covered with ciliated epithelium, and numerous glands are present in the mucous membrane. In other Mammals (G, I) it becomes more or less reduced, though often well-marked, consisting of two tubes lying at the base of the septum nasi, usually enclosed by separate cartilages (Marsupials, Edentates, Insectivores, Rodents, Carnivores, Ungulates). A branch of the olfactory nerve enters the tube posteriorly, and anteriorly the cavity of the organ communicates with the mouth through the incisive or naso-palatine canals. Rudiments of the organ exist even in Man (Fig. 163, C).

The function of Jacobson's organ may consist in bringing the food taken into the mouth under the direct control of the olfactory nerve.

### EYE.

As already mentioned (p. 154, Fig. 167, A and B), the optic nerve is developed from the stalk of an outgrowth of the primary

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[1] A curious apparatus exists in Cœcilians in connection with the nasal cavity and orbit. It consists of a fibrous capsule with muscles and a large gland, opening near the snout. Its function is not certainly known.

fore-brain known as the *primary optic vesicle*. It, therefore, like the olfactory lobe, represents a part of the brain.

In the adult brain, the optic nerve is seen to arise from the thalamencephalon, and three more or less sharply-differentiated portions of it may in most cases be distinguished; these are spoken of, from the proximal to the distal end respectively, as the *optic tract, chiasma,* and *nerve.*

The chiasma, that is, the crossing of the two optic nerves, is always present, though not always freely exposed, for it may retain a primitive position deeply embedded in the base of the brain, (*e.g.*, Cyclostomi, Dipnoi).

In most Teleosts the optic nerves simply overlie one another (Fig. 166, A), but in some of these Fishes (Clupea, Engraulis, Fig. 166, B), one nerve passes through a slit in the other, and this condition of things is gradually carried still further in Reptiles, until finally the fibres of the two nerves intercross in a very complicated manner (Fig. 166, C, D), giving rise to a sort of basket-work; this is finest and most delicate in Mammals, where its structure can only be analysed by comparing a series of sections. A more or less complete crossing of the fibres of each optic nerve may also take place more peripherally before they spread out in the retina.



Fig. 166.—CHIASMA OF THE OPTIC NERVES. (Semidiagrammatic.) A, chiasma characteristic of the greater number of Teleostei; B, Herring; C, Lacerta agilis; D, an Agama; E, a higher Mammal.

*Chi*, chiasma of the bundle of nerves lying centrally; *Ce*, *Ce¹*, *S*, *S¹*, lateral fibres; *Co*, commissure.

In contrast to the eyes of Invertebrates, which arise by a differentiation of the cells of the superficial epiblast, the sensitive elements of the Vertebrate eye correspond to a peripheral portion of the brain (Figs. 167, A and B).

As the primary optic vesicle grows outwards towards the outer skin of the embryo, the portion which connects it with the brain becomes constricted and by degrees loses its cavity, giving rise to a solid cord, from which the optic nerve is formed.

At the point where the vesicle touches the epiblast, the latter becomes thickened and the outer wall of the vesicle invaginated to form a double-walled cup, the *secondary optic vesicle* (Fig. 167, B). The inner and outer walls of the cup then become fused together, the former giving rise to the sensory epithelium of the *retina*, and the latter to the *pigment epithelium*. The fibres of the optic nerve are first differentiated in its retinal portion, and grow

centripetally towards the brain; centrifugal fibres also arise later.

In the course of further development, the epiblastic thickening mentioned above, which is often at first hollow, becomes separated from the epiblast, sinks more and more into the interior of the optic vesicle, and is differentiated to form the *crystalline lens* (Fig 167, B). The remaining space within the optic vesicle becomes filled by mesoblastic tissue, which grows in from the ventral side of the secondary optic vesicle through the so-called *choroid fissure*
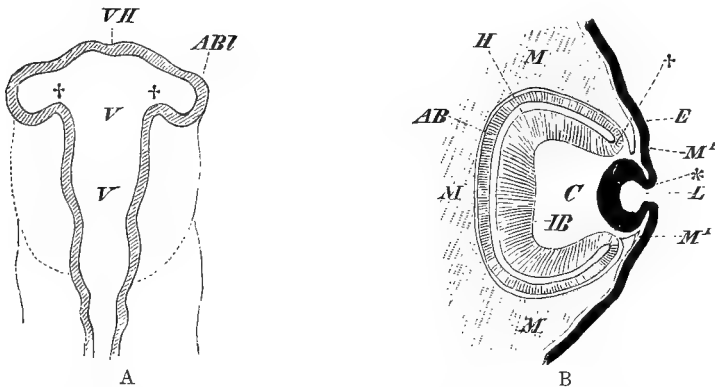


FIG. 167, A.—DIAGRAM SHOWING THE MODE OF FORMATION OF THE PRIMARY OPTIC VESICLES (*ABl.*)

*VH*, fore-brain ; *V, V*, ventricular cavity of the brain, which communicates freely with the cavities of the primary optic vesicles at ††.

B.—SEMIDIAGRAMMATIC FIGURE OF THE SECONDARY OPTIC VESICLE, AND OF THE LENS BECOMING SEPARATED OFF FROM THE EPIBLAST.

*IB*, inner layer of the secondary optic vesicle, from which the retina arises ; †, point at which the latter is continuous with the outer layer (*AB*), from which the pigment epithelium is formed ; *H*, remains of the cavity of the primary optic vesicle ; *L*, lens, which arises as a cup-shaped involution of the epiblast (*E*) ; *, point of involution of epiblast to form the lens ; *MM*, mesoblastic tissue, which at *M¹*, *M¹*, grows in between the outer epiblast and the lens as the latter becomes separated off, and which gives rise to the cornea as well as to the iris ; *C*, vitreous chamber of the eye, between the lens and retina, which later becomes filled by the vitreous humour.

and gives rise to the *vitreous humour* (Fig. 167, B), the bulk of which, as compared with the lens, gradually increases. Blood-vessels (vasa centralia nervi optici, arteria hyaloidea, tunica vasculosa lentis) also extend into the vesicle in the same manner.

The secondary optic vesicle is thus plentifully supplied with blood-vessels in its interior, and others arise at its periphery, where a definite vascular and pigmented membrane, the *choroid*, is formed from the surrounding mesoblast (Fig. 168).

Internally to the lens, the choroid gives rise to the *ciliary folds*, while more externally it passes in front of the lens to form

P

the *iris* (Fig. 168), which retains in the centre a circular or slit-like aperture, the *pupil*, through which the rays of light pass. The amount of light admitted is regulated by the dilator and constrictor (sphincter) muscles of the iris, which are able to increase or lessen the size of the pupil ; the iris thus serves as a screen to regulate the amount of light which enters the eye.

Not only is the size of the pupil inconstant, but the lens is also capable of undergoing considerable change in form, becoming more flattened or more convex, as the case may be. The former condition occurs when distant, the latter when near objects are looked at. This delicate *accommodating apparatus* is regulated by a *ciliary muscle* (*tensor choroideæ*) supplied by the oculomotor nerve, which arises in a circle all round the eye from the point of junction of the iris and sclerotic and is inserted along the peripheral border of the iris (Fig. 168).

Externally to the vascular layer of the choroid is a lymph-sinus with pigmented walls (*lamina fusca*) ; and externally to this, again, is a firm fibrous, partly cartilaginous, or even ossified layer, the *sclerotic*. The latter passes internally into the sheath of the optic nerve, which is continuous with the dura mater, and externally into the *cornea*, the outer surface of which is covered over by an epithelial layer continuous with the epidermis—the *conjunctiva*. The sclerotic and cornea together form a firm outer support for the eye, and thus, together with the gelatinous mass of the vitreous humour, guarantee the rigidity necessary for the physiological activity of the nerve end-apparatus. Between the cornea and iris there is a large lymph-space, the *anterior chamber* of the eye (Fig. 168), its contained fluid being called the *aqueous humour*. Other lymph-spaces are also present, *e.g.*, between the choroid and sclerotic.

The deep orbit, formed by the skull, serves as a further protection for the eye, as do also certain *accessory structures*, which may be divided into three categories, viz. :—



Fig. 168.—Diagram of a Horizontal Section through the Left Human Eye. (Seen from above.)

*Op*, optic nerve ; *OS*, sheath of optic nerve ; *MF*, blind-spot ; *Fo*, yellow spot (fovea centralis) ; *Rt*, retina ; *PE*, pigment epithelium of the retina ; *Ch*, choroid, with its lamina fusca (*Lf*) and vascular layer (*GS*) ; *Sc*, sclerotic ; *Co*, cornea ; *Cj*, conjunctiva ; *MD*, membrane of Descemet ; *CS*, canal of Schlemm (the dotted line should extend further through the sclerotic to the small oval aperture) ; *Ir*, iris ; *Lc*, ciliary ligament ; *C*, ciliary process ; *VK*, *HK*, anterior and posterior chamber of the eye ; *L*, lens ; *H*, hyaloid membrane ; *Z*, Zone of Zinn, *CP*, canal of Petit ; *Cv*, vitreous humour.

1. Eyelids (palpebræ).
2. Glandular organs.
3. Muscles, serving to move the eye-ball.

The eye-ball is thus formed of a series of concentric layers which are called from within outwards *retina*, *choroid* and *iris* (vascular layer), and *sclerotic* and *cornea* (skeletal layer). The first corresponds with the nervous substance of the brain, the second with the pia mater, and the third with the dura mater. The interior of the eye contains refractive media, the *lens* and *vitreous humour*. To these, certain *accessory structures* are added (pp. 216–220).

The relative development of the eye varies considerably amongst Verte-brates. It may reach a very high degree of perfection ; or may, on the other hand, undergo more or less degeneration in those animals which live in caves or burrows (e.g., *Fishes*—Amblyopsis spelæus, Typhlogobius ; *Amphibians*—Proteus, Gymnophiona ; *Snakes*—Typhlops : *Mammals*—Talpa, &c.). In Ammocœtes and Myxine the eye is hidden beneath the integument (see below), and in the Cetacean Platanista gangetica the eyes are extremely minute.

The retina will be dealt with after a description of the eyes of the various classes of Vertebrates has been given (p. 214).

In **Amphioxus** a simple pigment spot is present in the front wall of the "cerebral ventricle" (p. 157, and Fig. 219).

**Cyclostomes.**—The eye of Cyclostomes remains at a very low stage of development, not only as regards the structure of the retina, but also—in Myxinoids, in the absence of a lens and iris and of a differentiated sclerotic and cornea as well as of eye-muscles, and in the persistence of the choroid fissure. Moreover, the eye in Myxinoids and in the larval Ammocœte lies beneath the skin and subdermal connective tissue. In Petromyzon the skin covering the eye becomes thinned out at metamorphosis, and thus the animal, which was blind, or nearly blind, in the larval state, can see on reaching the adult condition : at the same time the eye becomes more highly organised, though the primary lumen in the lens (Fig. 167, B) does not entirely disappear.

**Fishes and Dipnoans.**—The eyes of all the true Fishes are, with few exceptions, of considerable relative size, and are formed on essentially the same plan as that described in the intro-ductory portion of this chapter.

The lens of Fishes, like that of all aquatic animals, is globular, and possesses therefore a high refractive index. It touches the cornea and fills up the greater part of the eyeball, so that only a small space is left for the vitreous humour. It differs from that of other Vertebrates in the fact that, in the condition of rest, it is accommodated for seeing near objects. In Teleosts accommodation apparently takes place by means of a process of the choroid, the *processus falciformis*. This extends into the vitreous humour towards the lens, around which it expands to form the so-called

*campanula Halleri* (Fig. 169). In the interior of this structure are nerves, vessels, and smooth muscle-fibres, and the latter possibly exert an influence on the lens, drawing it towards the retina. The processus falciformis is never large in Ganoids and is absent in Cyclostomes, Elasmobranchs, and Dipnoans : the question of accommodation in these Fishes is not understood.
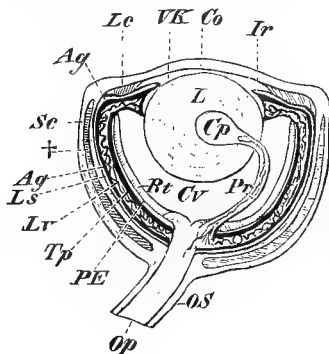


FIG. 169.—EYE OF A TELEOSTEAN.

*Op*, optic nerve ; *OS*, sheath of optic nerve ; *Rt*, retina ; *PE*, pigment epithelium ; *Tp*, tapetum ; *Lv*, lamina vasculosa ; *Ag*, argentea ; *Ls*, lamina supra-choroidea ; *Sc*, sclerotic, enclosing cartilage or bone (†) ; *Co*, cornea ; *Ir*, Iris ; *VK*, anterior chamber ; *L*, Lens ; *CV*, vitreous humour ; *Pr*, processus falciformis ; *Cp*, campanula Halleri.

Externally to the choroid proper, that is, between it and the lamina fusca, lies a silvery or greenish-gold iridescent membrane, the *argentea*. It extends either over the whole interior of the eye (Teleosts), or is limited to the iris (Elasmobranchs). A second layer with a metallic lustre, the *tapetum lucidum*, is present internally to the iridescent portion, and within this again is the chorio-capillaris of the choroid. No tapetum appears to be present in Teleostei or Petromyzon.

The so-called *choroid gland*, present only in Teleostei and Amia, consists of a network of blood-vessels (rete mirabile) which has the form of a cushion, lying near the entrance of the optic nerve, between the argentea and pigment epithelium of the retina : it thus has nothing to do with a " gland."

The sclerotic is usually extensively chondrified, and not unfrequently becomes calcified or ossified towards its junction with the cornea.

The eyeball is almost always surrounded by a gelatinous tissue, penetrated by connective-tissue fibres, and in Elasmobranchs it is usually articulated on its inner circumference with a rod of cartilage connected distally with the lateral wall of the skull.

**Amphibia.**—The eyes of Amphibians are proportionately smaller, and their form rounder than those of Fishes, but there are many points of close correspondence between them. This is true, for instance, as regards the more or less distinctly chondrified sclerotic, the slightly convex cornea, and the globular lens. In other important respects, however, the Amphibian eye is simpler than that of Fishes ; thus it is wanting in an argentea, a tapetum, a choroid gland, and a processus falciformis and campanula Halleri. The iris contains smooth muscle-fibres, and a true ciliary muscle is present in the whole series of animals from this point onwards, though not strongly developed in Amphibians. The pupil is usually round, but may be angular.

The eyes of Proteus and of the Gymnophiona, as already mentioned, always lie more or less deeply beneath the skin ; they are very small, and are much degenerated. In Proteus the crystalline lens and iris are both wanting, and the vitreous humour is only slightly developed.

**Reptiles and Birds.**—In these also, the sclerotic is in great part cartilaginous, and in Lizards and Chelonians it is provided with a ring of delicate bony *sclerotic plates* around the external portion (Fig. 170). Many fossil Reptiles and Amphibians possessed similar plates, as do also existing Birds (Fig. 171) ; in Birds horseshoe- or ring-shaped bony structures are also usually present close to the entrance of the optic nerve.

Fig. 170. — Eye of *Lacerta muralis*, showing the Ring of Bony Sclerotic Plates.

The eyeball of Reptiles has a globular form (Fig. 170), while that of Birds, more especially nocturnal Birds of prey (Owls), is more elongated and tubular, an external larger segment being sharply marked off from an internal smaller one : moreover the whole eye is relatively larger. (Fig. 171). The outer portion is bounded externally by the very convex cornea and encloses a large anterior chamber as well as a complicated ciliary muscle composed of striated fibres. This muscle is also transversely striated in Reptiles, in which—especially in Chelonians, it is always well developed, though not to such an extreme degree as in Birds.

In Reptiles (Lizards, for instance) a tapetum may be developed, but an argentea and choroid gland are never present; all these parts are wanting in Birds. A structure which is homologous with the processus falciformis of Fishes is, however, present in most Reptiles and in Birds. Absent in Hatteria and the Chelonia, this so-called *pecten* is largely developed in Birds [1] (Fig. 171), and may extend from the point of entrance of the optic nerve to the capsule of the lens, but



Fig. 171.—Eye of an Owl.

*Rt*, retina ; *Ch*, Choroid ; *Sc*, sclerotic, with its bony ring at † ; *CM*, ciliary muscle ; *Co*, cornea ; *VN*, point of junction between sclerotic and cornea ; *Ir*, iris ; *VK*, anterior chamber ; *L*, lens ; *Cr*, vitreous humour ; *P*, pecten ; *Op*, *OS*, optic nerve and sheath. The dotted line passing across the broadest portion of the circumference of the eye divides the latter into an inner and an outer segment.

[1] In Apteryx the pecten disappears during development.

as a rule does not reach so far. In Birds it is always more or less folded, and consists mainly of a closely-felted network of capillaries. In both Reptiles and Birds, the pecten appears to be important in the nutrition of the contents of the eyeball and of the retina : it has nothing to do with accommodation.

The iris, which is regulated by striated muscle, by means of which it is able to respond very quickly to visual impressions, is often brightly coloured, and this colour is due to the presence, not only of pigment, but also of coloured fat globules.

The pupil is as a rule round, but in many Reptiles and in Owls has the form of a vertical slit.

**Mammals.**—In Mammals the eyeball is always more completely enclosed within the bony orbit than is the case in most other Vertebrates, and this may partially account for the fact that, except in Monotremes, the sclerotic no longer shows traces of cartilage or bone, but is entirely of a fibrous character (Fig. 168).

With the exception of aquatic Mammals, in which it is somewhat flattened, the cornea is moderately convex, and the whole eyeball is of a more or less rounded form.

A tapetum lucidum, consisting either of cells or fibres, exists in the choroid of numerous Mammals, and gives rise by interference to a glistening appearance when seen in the dark (Carnivores, Ruminants, Perissodactyles, &c.).

Certain structures homologous with the processus falciformis and pecten are present in Mammals in the embryo only.

The ciliary muscle consists of smooth elements.

The external surface of the lens is less convex than the internal, which latter lies in the so-called fossa patellaris of the vitreous humour.

The pupil is not always round, but may be transversely oval (Ungulates, Kangaroos, Cetaceans), or slit-like and vertical (*e.g.*, Cat).

### Retina.

The fibres of the optic nerve, which pass into the eyeball at a right or acute angle, cross one another at the point of entrance, and are then distributed to the sensitive elements of the retina. The latter is thus thickest at the point of entrance of the nerve, which is known as the " blind spot " (Fig. 168), and gradually decreases in thickness towards the ciliary processes, until, at the point of origin of the iris, it consists of a single layer of cells.

The retina is bounded externally by a structureless hyaline membrane (*limitans externa*),[1] while on its inner side it is covered by the *hyaloid membrane,* which, strictly speaking, belongs to the vitreous humour. The retina is quite transparent in the fresh condition, and consists of two portions which are histologically and physiologically quite distinct: they are, a *supporting*

[1] The membrana limitans encloses the entire retina externally in the embryo, but later the rods and cones come to project through it (*see* Fig. 172).

*part* and a *nervous part.* The former is stretched as on a frame between the limitans externa and hyaloid membrane.

The nervous elements are arranged in the following concentric layers :—

I. *Developed from the internal layer of the secondary optic vesicle.*
A. *Cerebral layer.*
   1. Layer of nerve-fibres (of optic nerve).
   2. Layer of ganglion-cells.
   3. Inner reticular layer.
   4. Granular layer (inner).
   5. Outer reticular or subepithelial layer.
B. *Epithelial layer.*
   6. Layer of visual cells (outer granular layer with the rods and cones).

II. *Developed from the external layer of the secondary optic vesicle.*
   7. Pigment epithelium (retinal epithelium).

It seems probable that the various nerve-cells of the retina are not directly connected with one another, but are only contiguous.
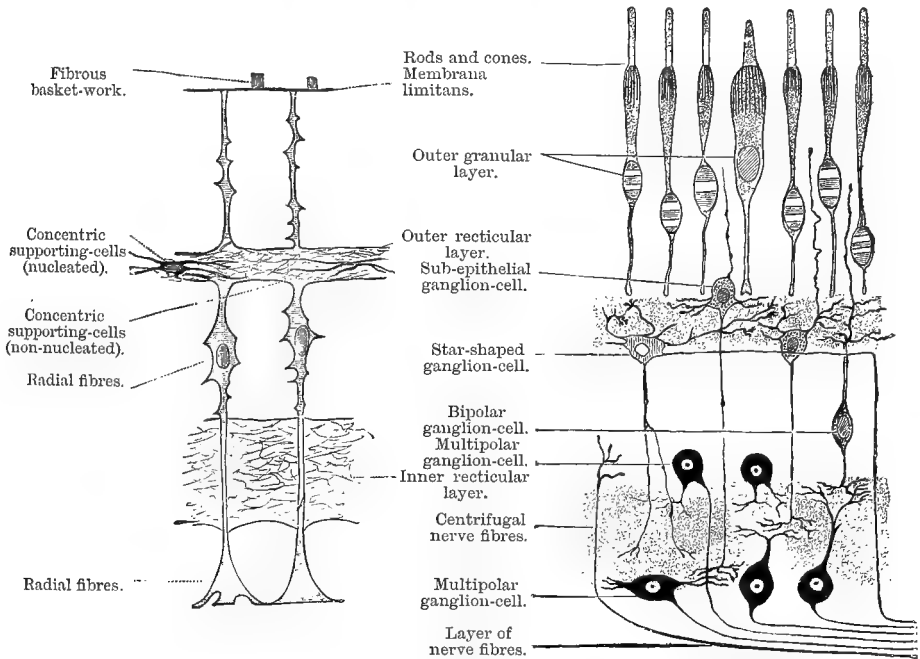


Fig. 172.—Diagram of the Elements of the Retina. (Supporting elements on the left, and nervous elements on the right.) After Ph. Stöhr.

These layers are so arranged that the nerve-fibres lie next to the vitreous humour, that is, internally, while the rods and cones

are situated towards the choroid, or are external. Thus the terminal elements of the neuro-epithelium are turned away from the rays of light falling upon the retina, and the rays must therefore pass through all the other layers before they reach the rods and cones.

Fishes possess the longest, Amphibians the thickest rods, so that in the latter there are only about 30,000 to a square millimetre, while in Man there are from 250,000 to 1,000,000.

In Fishes the rods far exceed the cones in number, while in Reptiles and Birds the reverse is the case. The cones of many Reptiles and all Birds are distinguished by the presence of brightly coloured oil-globules, which are also present in those of Marsupials.

In the centre of the retina of higher Vertebrates there is a specially modified region of most acute vision, called the *yellow-spot* (*fovea centralis* or *macula lutea*). It is due to the thinning-out of all the layers except that of the rods and cones, and even the rods disappear, only the cones persisting (Fig. 168).


## Accessory Organs in Connection with the Eye.

### (*a*) EYE-MUSCLES.

The movement of the eyeball is always (except in Myxinoids, comp. p. 211) effected by six muscles, four of which are known as the *recti* (superior, inferior, anterior or internal, and posterior or external), and two as the *obliqui* (superior and inferior). The former, which arise from the inner portion of the orbit, usually from the dural sheath of the optic nerve, together circumscribe a pyramidal cavity, the apex of which lies against the inner portion of the orbit, while the base surrounds the equator of the eyeball, where the muscles are inserted into the sclerotic.

Both the oblique muscles usually arise from the anterior or nasal side of the orbit, and as they respectively pass from this region dorsally and ventrally in an equatorial direction round the eyeball, they constitute a sort of incomplete muscular ring.

A deviation from this arrangement is seen in Mammals, in which the superior oblique has gradually come to arise from the inner part of the orbit, and then passes forwards towards its anterior (internal) angle, where it becomes tendinous, and passes through a fibro-cartilaginous pulley (trochlea) attached to the upper border of the orbit, on the frontal bone. Hence it is sometimes called the trochlear muscle. From this point it changes its direction, and becomes reflected obliquely outwards and backwards to the globe of the eye.

Besides these six muscles, others are usually present which are known as the *retractor bulbi* (best developed in Ungulates), the *quadratus* (*bursalis*), and the *pyramidalis*. The last two are connected with the nictitating membrane (see p. 217), and are present in Reptiles and Birds. All three are supplied by the abducent nerve (comp. p. 184).

## (b) EYELIDS (PALPEBRÆ).

In Fishes and other lower aquatic forms the upper and lower eyelids are usually very rudimentary, having at most (e.g., Elasmobranchs) the form of stiff folds of the skin ; and in all Vertebrates below the Mammalia they never reach a very high stage of development.  They are lined on the surface looking towards the eyeball by a continuation of the epidermis, the conjunctiva (p. 210), and in the Ichthyopsida and Sauropsida are usually not sharply marked off from the rest of the skin, being capable of no, or only of very slight, movement.[1]

In Mammals, the eyelids, more particularly the upper one, are extremely movable, and are provided with hairs (eyelashes) on their free margin.  In their interior a hard body, the so-called " lid-cartilage " is developed, and they are closed by a circular muscle which surrounds the whole slit between the lids ; a levator is also present in the upper eyelid.  In Sauropsida and many Mammalia (e.g., Ungulates) there is a depressor of the lower lid.

The want, or comparatively slight development of upper and lower eyelids in Vertebrates below the Mammalia is compensated for in certain forms, at any rate to a certain extent, by the presence of a nictitating membrane.  This "third eyelid" differs from the others in having nothing to do with the outer skin proper, consisting simply of a reduplicature of the conjunctiva, and being regulated by special muscles (see p. 216).

The nictitating membrane, which is represented in certain Elasmobranchs (e.g., Carcharias, Galeus, Zygæna, Mustelus, comp. p. 143) and which often encloses a cartilage, is situated within the lower eyelid, or it may lie more towards the anterior angle of the eye.  The former condition is seen, e.g., in Anurans, and the latter in Birds, in which a third eyelid is so largely developed as to be capable of covering the whole freely exposed portion of the eyeball.  In Reptiles and Mammals it always lies in the anterior angle of the eye ; in Primates it becomes reduced to a small, half-moon-shaped fold (plica semilunaris), but in Monkeys and certain races of Mankind traces of the cartilage are present.

### (c) GLANDS.

The glands in connection with the eye are : (1) the lachrymal, (2) the Harderian, or gland of the nictitating membrane, and (3) the Meibomian glands.

The secretions of all these serve to keep the free surface of the eyeball moist, and to wash away foreign bodies.  In Fishes and

[1] In many Reptiles and Birds the upper eyelid, is supported by a membrane-bone or fibro-cartilage.  In Geckos, Amphibænians and Snakes the two eyelids grow together to form a transparent membrane overlying the eye, and this comes away with the rest of the outer part of the skin when the latter is shed.

Dipnoans,[1] the outer medium appears to suffice for this purpose, but the first attempt of a Vertebrate to exchange an aquatic for an aërial existence necessitated the development of a secretory apparatus in connection with the eye.
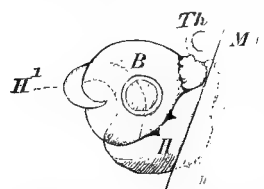


Fig. 173. — Harderian Gland (*H, H*[1]) and Lachrymal Gland (*Th*) of *Anguis fragilis*.

*M*, muscle of jaw ; *B*, eyeball.

Thus in Urodeles a glandular organ is developed from the conjunctival epithelium along the whole length of the lower eyelid ; in Reptiles this becomes more developed in the region of the anterior and posterior angles of the eye, and the original connecting bridge gradually disappears : thus two glands are developed from the primitively single one, each of which becomes further differentiated both histologically and physiologically. From one is formed the *Harderian gland*, which always lies at the anterior angle of the eye, surrounding to a greater or less extent the antero-ventral portion of the eyeball, while the other gives rise to the *lachrymal gland*[2] (Figs. 173 and 175). The latter retains throughout life its primitive position at the posterior angle of the eye, and even in Birds lies in the region of the lower eyelid ; it is supplied by the second division of the trigeminal. In Mammals it becomes gradually further subdivided, and extends into the region of the upper eyelid, so that its ducts open above the eye into the upper conjunctival sac (Fig. 175, A & B). Nevertheless, even in the Primates, more or fewer ducts are present which open into the lower conjunctival sac, and thus the primitive position of the lachrymal gland is indicated.

A well-differentiated Harderian gland is present from the



Fig. 174.—Diagrammatic Transverse Vertical Section through the Eye of a Mammal.

*Op*, optic nerve ; *B*, eyeball ; *Fo, Fo*, upper and lower conjunctival sac ; *LH, LH*, outer skin of the eyelids, which at the free edges of the latter at † becomes continuous with the conjunctiva ; *T*, the so-called tarsal fibro-cartilages, in which the Meibomian glands (*MD*) lie embedded, the latter opening at * ; *H, H*, eyelashes.

tailless Amphibia to the Mammalia, but is very rudimentary in the Primates.

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[1] Comp. p. 17.
[2] A lachrymal gland is absent in Crocodiles and Snakes.

The *Meibomian glands*, belonging to the group of sebaceous glands, are confined to the Mammalia, and lie embedded in the
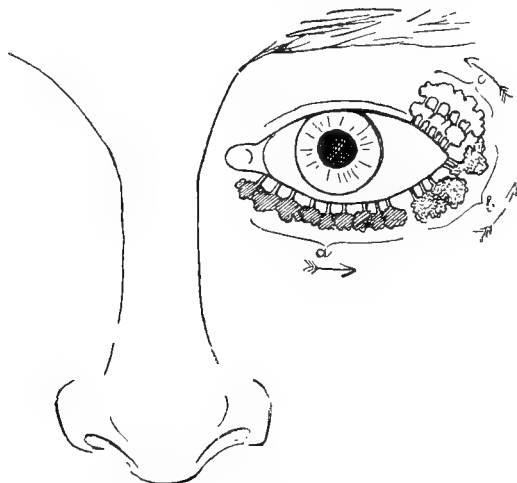


Fig. 175A.—Diagram to illustrate the shifting of the Lachrymal Gland which has taken place in the course of Phylogeny.

The gland shifts in the direction of the arrows; *a*, its position in the Amphibia; *b*, in Reptiles and Birds, and occasionally in Man, in which case it may be regarded as atavistic; *c*, normal position in Man.

substance of the eyelids in the form of branched tree-like tubes or clustered masses. They open on the free edge of the lid, and produce a fatty secretion. Certain modified sweat-glands known as
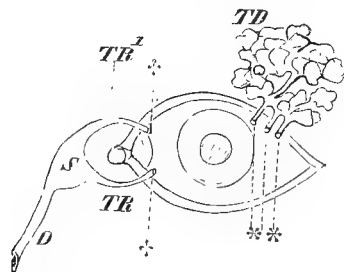


Fig. 175B.—Diagram of the Lachrymal Apparatus of Man.

*TD*, lachrymal gland, divided up into several portions; **, ducts of the lachrymal gland; ††, puncta lachrymalia; *TR*, *TR*[1], upper and lower lachrymal canals; *S*, lachrymal sac; *D*, naso-lachrymal duct.

the *glands of Moll* are also present immediately within the eyelids of Mammals.

The naso-lachrymal duct, which conducts the lachrymal secretion into the nose, has already been referred to (p. 201).

In the Cetacea, the lachrymal and Meibomian glands, as well as the naso-lachrymal duct, are wanting, and a lachrymal duct is absent in the Otter, Seal, and Hippopotamus.   In the two last-mentioned animals the lachrymal gland is much reduced : in Manis javanica there are no Meibomian glands, and in the Mole the entire lachrymal apparatus has undergone reduction.   ·

## AUDITORY ORGAN.

It is very probable that the auditory organ, like the organs of smell and taste, has been derived primitively from a modified integumentary sense-organ.   It is developed from an invagination
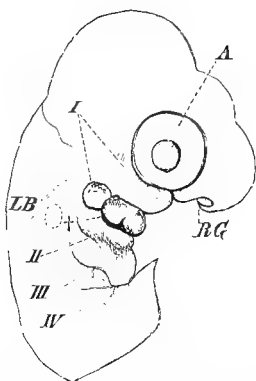


FIG. 176.—HEAD AND ANTERIOR PORTION OF BODY OF A CHICK. (In part after Moldenhauer.)

*RG*, olfactory pit ; *A*, eye ; *I* to *IV*, first to fourth visceral arches ; †, point at which the external auditory passage begins to be formed ; *LB*, primitive auditory vesicle seen through the wall of the head.
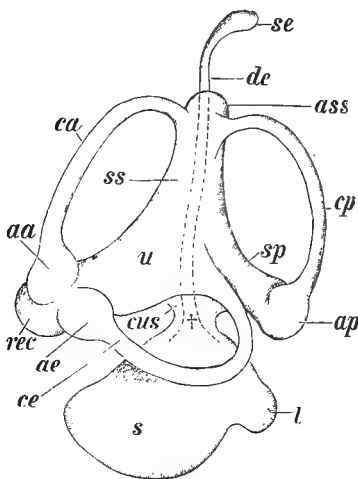


FIG. 177.—SEMIDIAGRAMMATIC FIGURE OF THE MEMBRANOUS LABYRINTH OF VERTE-BRATES.   (Seen from the outer side.)

*u*, utriculus ; *rec*, recessus utriculi ; *sp*, sinus posterior utriculi ; *s*, sacculus ; *l*, recessus sacculi (lagena) ; *cus*, utriculo-saccular canal ; *de*, *se*, ductus and saccus endolym-phaticus, the former arising from the sacculus at † ; *ss*, sinus utriculi superior ; *ass*, apex of the same ; *ca*, *ce*, *cp*, anterior, external, and posterior semicircular canals; *aa*, *ae*, *ap*, the corresponding ampullæ.

of the ectoderm on either side of the primary hind-brain : this be-comes separated off to form a vesicle (Fig. 176), and its epithelium is differentiated into elongated cells of *sensory epithelium* pro-vided with hair-like processes (Figs. 178 A and B) separated by *supporting cells.*   The sensory cells are surrounded by a nerve-network, and are not continuous with the nerves as in the case of the olfactory cells (p. 197).

Like the other higher sense-organs, the paired auditory organ

of Vertebrates is situated in the region of the head, between the origins of the trigeminal and vagus nerves. After the vesicle of each side has become separated off from the epiblast and connected with the brain by means of the auditory nerve (which arises in connection with a peripheral ectodermic ganglion and then grows centripetally to the brain), it sinks deeper and deeper into the mesoblastic tissue of the skull : it then loses its original pyriform or rounded shape, and becomes divided into two parts, called respectively the *utriculus* and *sacculus* (Fig. 177). From the former
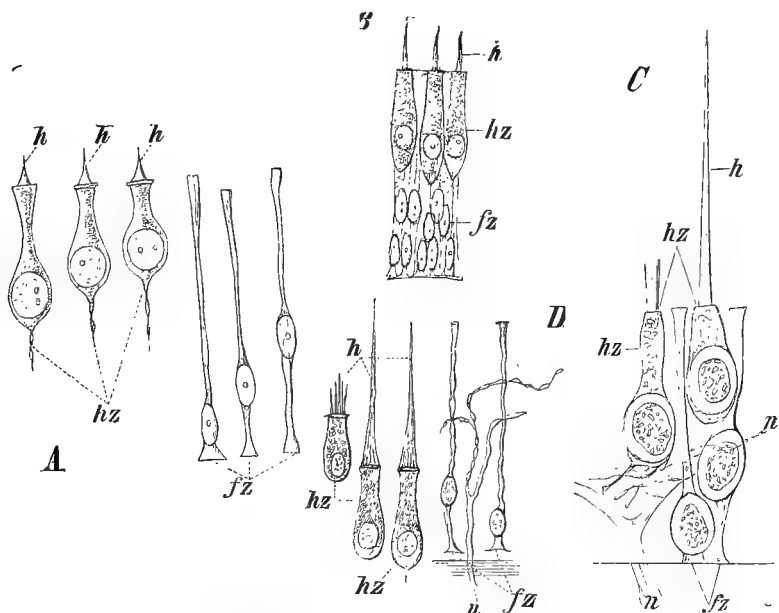


FIG. 178A.—ISOLATED ELEMENTS OF THE MEMBRANOUS LABYRINTH OF VARIOUS VERTEBRATES. (After G. Retzius.)

A, from the macula acustica communis of *Myxine glutinosa* ; B, from the macula acustica neglecta of *Raia clavata* ; C, from the crista acustica of an ampulla of *Linedon (Amblystoma) mexicanus* ; D, from the crista acustica of the anterior ampulla of *Roma esculanta*.

hz, hair-cells with auditory hairs (h) ; fz, thread-like cells; n,n, dividing nerve. On the left side of D the auditory hair has become broken up into its constituent fibres.

the *semicircular canals* become developed, while from the latter the tube-like *ductus endolymphaticus* and the *lagena* (*cochlea*) are formed.

The whole of this complicated apparatus constitutes the *internal ear* or *membranous labyrinth*. It becomes surrounded secondarily by mesoblastic tissue, with which it is at first in close contact. A process of absorption then takes place in the innermost layers of the mesoblast, and thus a space is developed which closely

repeats the form of the membranous labyrinth, as does also the
mesoblast which encloses this space  and which later becomes
chondrified, and often also ossified.  A *membranous* and a *bony laby-
rinth* can thus be distinguished, and between them is a cavity
(*cavum perilymphaticum*) filled with a lymph-like fluid (*perilymph*).
The cavity within the membranous labyrinth, which also contains a
fluid (*endolymph*), is spoken of as the *cavum endolymphaticum*.

Except in Cyclostomes, three semicircular canals are always
present, and these lie in planes at right angles to one another.
They are distinguished  as the *anterior vertical*, the *posterior
vertical*, and the *horizontal* (*external*) canals (Fig. 177).    The first
and last-named  arise from the portion of the utriculus known as
the recessus utriculi, and each has a vesicle-like swelling or *ampulla*
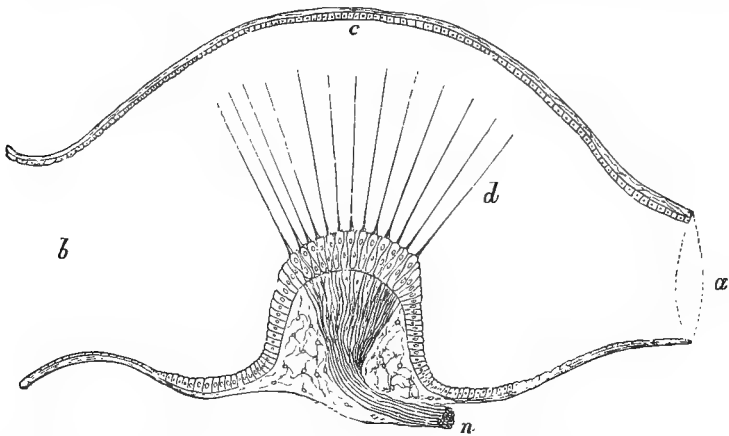


FIG. 178B.—LONGITUDINAL SECTION OF AN AMPULLA OF GOBIUS. (The exact form
of the epithelium of the crista is not indicated.)    After Hensen.

*n*, the nerve  passing into the  connective-tissue of the crista ;  *a*, base of semi-
circular canal ;  *b*, point of opening of the ampulla into the utriculus ;  *c*, the
epithelium on the free wall of the ampulla ;  *d*, the auditory hairs.

at its origin.    The posterior canal also arises with an ampulla from
a prolongation of the utriculus (sinus posterior).    The other end of
the horizontal canal opens by a funnel-shaped enlargement into the
utriculus, while that of the anterior and of  the posterior  canal
fuse together to form a common tube, the so-called *canal commissure*
(sinus superior), which also opens into the utriculus.

Concretions composed mainly of carbonate of lime are present
in the regions of the various nerve end-plates of the auditory
organ in all Vertebrates.    These *otoliths* present the greatest
variety both in form and size.    The largest and most massive ones
are seen in Teleosts.    They either consist of a single  mass, or are
arranged in groups in different regions of the labyrinth.

The sensory epithelium, to which the branches of the auditory nerve are distributed, is situated in the following parts of the membranous labyrinth : (1) the three ampullæ of the canals, in each of which the auditory cells are situated on a ridge (*crista acustica*) projecting into the lumen (Fig. 178B) ; (2) a large *macula acustica* in the utriculus : this is continued into the recessus utriculi
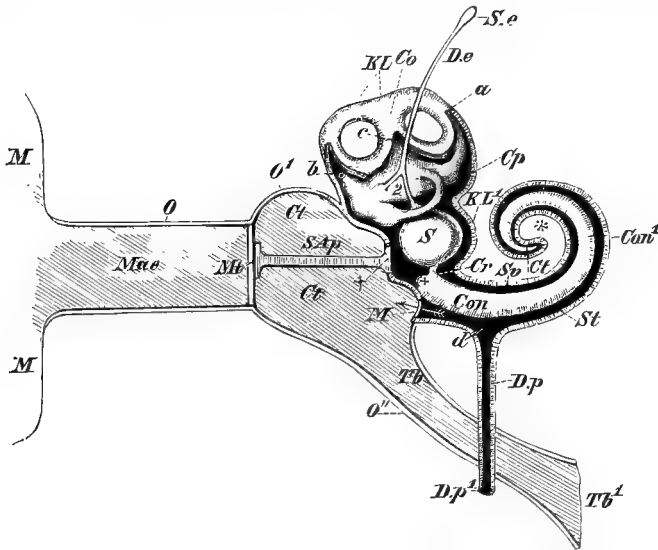


FIG. 179.—DIAGRAM OF THE ENTIRE AUDITORY ORGAN OF MAN.

*External Ear.*—M, M, pinna ; *Mae*, external auditory meatus ; O, wall of latter ; Mt, tympanic membrane.

*Middle Ear.*—Ct, Ct, tympanic cavity ; O¹, wall of same ; SAp, sound-conducting apparatus, indicated by a rod, representing the auditory ossicles, the end of the rod marked † corresponds to the stapes, which closes up the fenestra ovalis ; M, fenestra rotunda ; Tb, Eustachian tube ; Tb¹, its opening into the pharynx ; O'', its wall.

*Internal Ear*, with the greater part of the bony labyrinth (KL, KL¹) removed. – S, sacculus ; a, b, the two vertical canals, one of which (b) is shown cut through ; c, Co, commissure of the canals of the membranous and bony labyrinths respectively ; S.e, D.e, saccus and ductus endolymphaticus ; the latter bifurcates at ·2 ; Cp, cavum perilymphaticum ; Cr, canalis reuniens ; Con, membranous cochlea, which gives rise to a blind sac at ·+ ; Con¹, bony cochlea ; Sv and St, scala vestibuli and scala tympani, which at * pass into one another at the cupula terminalis (Ct) ; D.p, ductus perilymphaticus, which arises from the scala tympani at d, and opens at D.p¹. The horizontal canal is seen between 2 and S.

as well as into the sacculus and lagena, or rudiment of the cochlea, which arises from the sacculus ; (3) the rudimentary *macula acustica neglecta*, which in Fishes, Birds, and Reptiles is situated on the floor of the utriculus close to the sacculo-utricular canal. In Amphibians it lies on the inner side of the sacculus, and in Mammals undergoes a gradual reduction and may even become

obliterated. The several portions of the sensory plate or macula acustica, which are originally continuous, become later disconnected from one another, and except in Cyclostomes are seen as separate maculæ acusticæ.

The higher we pass in the Vertebrate series, the greater share does the mesoblast take in the formation of the auditory organ. At first—that is, in Fishes—the membranous labyrinth or internal ear lies close under the roof of the skull, and is thus easily accessible to the waves of sound, which are conducted partly through the operculum (when present), and partly through the gill-slits or spiracle. As we pass to the higher animals, however, the auditory organ gradually sinks further and further inwards from the surface, so that a new method for conducting the sound-waves becomes necessary, and certain accessory structures are developed (Fig. 179). A canal, the *external auditory passage* or *meatus*, passes inwards from the surface ; this opens into a spacious chamber, the *tympanic cavity*, in which are situated the *auditory ossicles*, and which is connected by the *Eustachian tube* with the pharynx. The whole of this canal, which is divided into outer and inner portions (*external* and *middle ear*) at the junction of the external auditory passage and tympanic cavity by a vibratory membrane, the *tympanic membrane*, lies in the position of the first embryonic visceral (hyoid or spiracular) cleft. From Reptiles and Birds onwards the first indications of a *pinna* (that is, the part of the external ear which projects from the head) are seen, but this only reaches a full development in Mammals.

**Cyclostomes.**—In Petromyzon there are only two (the vertical) semicircular canals, and in Myxine only one canal is present, which, as it possesses two ampullæ, probably represents the two fused together (Fig. 180A).

**Fishes and Dipnoans.**—The auditory organ of all the true Fishes (Fig. 180A[1]–C) follows the general plan given above, and the same may be said for all higher Vertebrates. Almost without exception we meet with a division into a *pars superior*—represented by the *utriculus* and *semicircular canals*, which remains essentially much in the condition already described, and a *pars inferior*—constituted by the *sacculus* and *lagena*, which gradually becomes more differentiated, and attains to a higher and higher degree of development and functional perfection. In Fishes the lagena consists simply of a small knob-like appendage of the sacculus, which opens freely into the main cavity of the latter by means of the sacculo-cochlear canal : it is absent in Chimæra. The utriculus and sacculus also communicate with one another by the sacculo-utricular canal. In Elasmobranchs the ductus endolymphaticus opens dorsally on the posterior part of the head, and is thus in free communication with the sea-water.
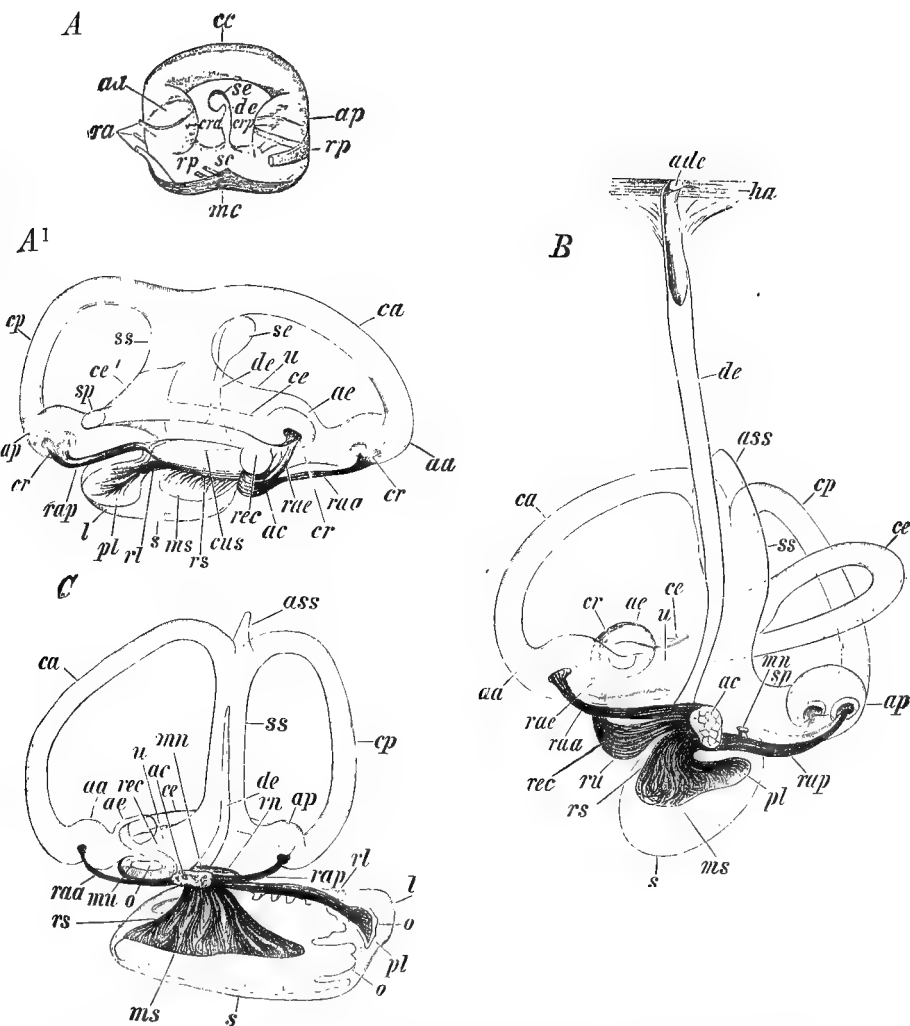
Fɪɢ. 180—Membranous Labyrinth of Various Fishes (after G. Retzius).
A, *Myxine glutinosa*, from the inner side.

*sc*, saccus communis ; *aa*, *ap*, anterior and posterior ampulla ; *cc*, canalis communis ; *de*, ductus endolymphaticus ; *se*, saccus endolymphaticus ; *mc*, macula acustica communis ; *cra*, crista acustica of the anterior, and *crp*, of the posterior ampulla ; *ra*, *rp*, anterior and posterior branches of the auditory nerve.

A[1], *Acipenser sturio*, outer side ; B, *Chimæra monstrosa*, inner side ; C, *Perca fluviatilis*, inner side.

*u*, utriculus ; *ss*, *sp*, sinus utriculi superior and posterior ; *ass*, apex of the sinus superior ; *rec*, recessus utriculi ; *aa*, *ae*, *ap*, anterior, external, and posterior ampulla ; *ca*, *cp*, *ce*, anterior, posterior, and horizontal (external) semicircular canals ; *s*, sacculus ; *cus*, utriculo-saccular canal ; *de*, ductus endolymphaticus, which in B opens externally through the skin *ha* at *ade* ; *se*, saccus endolymphaticus ; *l*, lagena ; *mu*, macula acustica of the recessus utriculi ; *cr*, crista acustica of the ampullæ ; *ms*, macula acustica of the sacculus ; *mn*, macula acustica neglecta ; *pl*, papilla acustica of the lagena ; *ac*, auditory nerve ; *raa*, *rae*, *rap*, *ru*, *rs*, *rl*, *rn*, the various branches of the same ; *o* (in C), otoliths (in the recessus utriculi, sacculus, and lagena.)

In Chimæroids, Ganoids, Teleosts and Dipnoans, the auditory capsules are not completely surrounded by cartilage or bone, the perilymphatic and cranial cavities only being separated by a fibrous partition.

In certain Teleosts (Siluroidei, Gymnotidæ, Characinidæ, Gymnarchidæ, Cyprinoidæ) the auditory organ comes into relation with the air-bladder by means of a chain of bones (" Weberian ossicles ") derived from certain parts of the four anterior vertebræ and corresponding pairs of ribs, and by this means the relative fulness of the air-bladder can be appreciated by the Fish. Connections between processes of the air-bladder and the internal ear are also met with in several other Teleosts.

The auditory organ of the Dipnoi most nearly resembles that of Elasmobranchii, and more particularly that of Chimæra.

**Amphibia.**—The membranous labyrinth of Amphibians resembles that of Fishes and Dipnoans in many respects, but important differences are seen, more particularly as regards the lagena, which, especially in the Anura, becomes further constricted off from the sacculus and reaches a higher stage of development. Traces of a papilla acustica lagenæ lying within the lagena are met with in the Myctodera, and even in Menopoma and Siredon. In the Anura (Fig. 181) a higher condition is seen in the presence of a small ridge-like outgrowth in the interior of the thickened lagena on which a definite region, supported by cartilage, corresponds to the *basilar membrane* of higher types ; this bears another patch of nerve endings—the *papilla acustica basilaris*.

The ductus endolymphaticus, as in certain Teleosts, may give rise to large sac-like enlargements containing calcareous matter and lie close to its fellow, either on the dorsal surface only, or on both dorsal and ventral sides of the brain. The latter is the case in Anura, for instance, in which the sac extends as an unpaired structure along the whole vertebral canal dorsally to the spinal cord, giving rise to paired outgrowths extending through the intervertebral foramina and forming the characteristic *calcareous bodies* situated close to the spinal ganglia. These are lined by pavement epithelium and are plentifully supplied with capillaries : they are not glandular, as was formerly supposed.

A further advance in structure as compared with Fishes is seen in the gradual differentiation of a *middle ear*. In the outer wall of the auditory capsule is a membranous space, the *fenestra ovalis*, which is plugged by a cartilaginous *stapedial plate ;* and from the latter a rod-like cartilage or bone, the *columella*, usually extends outwards towards the quadrate (p. 84). A *tympanic cavity*, with a *tympanic membrane* supported by a ring of cartilage lying on the level of the skin, and a *Eustachian tube* opening into the pharynx and corresponding phylogenetically to the hyoid cleft of Fishes, are met with in most Anura, in which also the columella is more perfect, consisting of a bony and cartilaginous rod

expanded distally to fit against the tympanic membrane. The columella is wanting in certain Urodeles (*e.g.*, Triton). A membranous *fenestra rotunda* in the outer wall of the auditory capsule is present in most Amphibians and in all higher Vertebrates in addition to the fenestra ovalis.

The ear of the Gymnophiona resembles that of the Urodela, but the membranous labyrinth shows further complications.
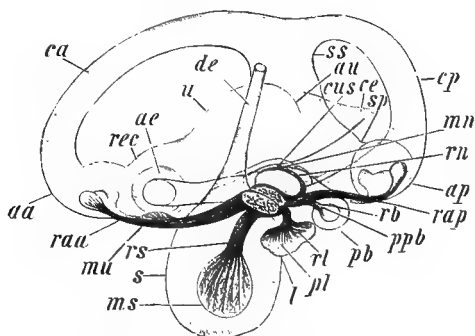


FIG. 181.—RIGHT MEMBRANOUS LABYRINTH OF *Rana esculenta*, from the inner side. (After G. Retzius.)

*au*, aperture of utriculus ; *l*, lagena cochleæ ; *pb*, pars basilaris cochleæ ; *cus*, utriculo-saccular canal ; *mn*, *ms*, *mn*, macula acustica recessus utriculi, sacculi, and neglecta ; *pl*, *ppb*, papilla acustica lagenæ and basilaris ; *rua*, *rap*, *rs*, *rn*, *rl*, *rb*, branches of auditory nerve to the anterior and posterior ampullæ, sacculus, macula neglecta, lagena, and pars basilaris. (Other letters as in Fig. 180, A¹–C.)

**Reptiles and Birds.**—In Chelonians, the auditory organ shows many points of resemblance to that of Urodeles; and in all Reptiles and Birds the chief modifications are confined to the lagena or *cochlea*, which gradually shows a higher condition of development in passing from Chelonians and Snakes to Lizards and Crocodiles. In Chelonians, the cochlea grows out in the form of a short canal ; in Crocodiles and Birds this canal is considerably longer, and at the same time it becomes slightly coiled (Figs. 182 and 183). A more marked differentiation also gradually takes place in the membrana basilaris and the papilla acustica basilaris. Both become more and more elongated ; and, at the same time, distinct indications of *scalæ tympani* and *vestibuli* are seen. (Compare the description of these parts on p. 232.)

In the Lacertilia the most varied types of auditory organ are met with ; in many (Phrynosoma, Pseudopus, Anguis), the membrana basilaris is hardly more highly developed than in Ophidia. In Iguana, an advance towards Lacerta and the other higher Lizards is to be noticed . the membrana basilaris is longer, though the lagena with its papilla is not so prominent. In Acantias and Platydactylus this state of things is carried still further, and finally the more highly developed auditory organ of Plestiodon and Egerina

leads up to that of Crocodilia. Thus there is a continuous and an unbroken series from the lower forms to the higher.

The structure of the auditory organ of Hatteria shows many striking peculiarities : it thus, like that of Chamæleo, occupies an isolated position.

While the cochlea gradually becomes more independent of the sacculus, the latter shows the greatest variety both as to form and size in the different types. Thus, for instance, it is usually very small in Birds, while in Lizards (*e.g.*, Lacerta) it is of considerable size
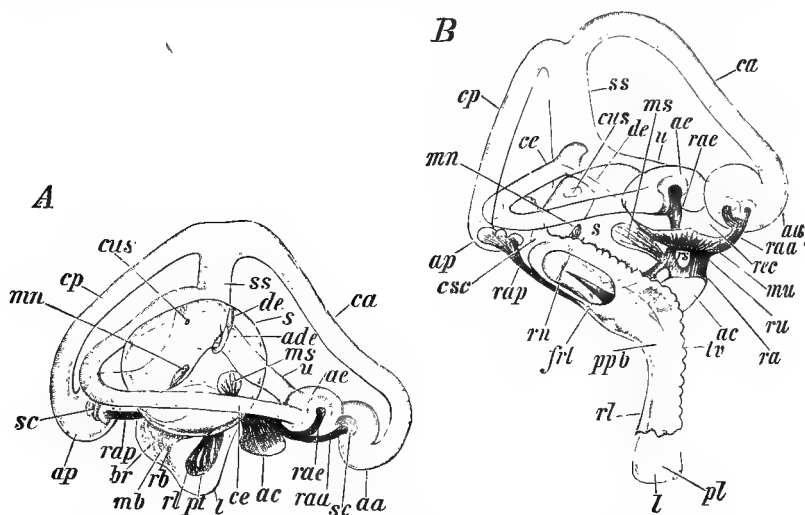


FIG. 182.—RIGHT MEMBRANOUS LABYRINTH OF A, *Lacerta viridis*, AND B, *Alligator mississipiensis*, from the outer side. (After G. Retzius.)

*ade*, aperture of the ductus endolymphaticus ; *csc*, sacculo-cochlear canal; *frt*, foramen recessus scalæ tympani ; *tv*, tegmentum vasculosum ; *sc*, septum cruciatum ; *mb*, membrana basilaris. (Other letters as in Figs. 180 and 181.)

The aperture of communication between the utriculus and sacculus persists, though it gradually becomes narrowed, as does also that between the sacculus and cochlea. The connection between these latter may be drawn out to form a canal (*canalis reuniens*), and this is particularly the case in Birds ; in Crocodiles an intermediate condition between Birds and Lizards is seen. The membranous labyrinth of Birds, however, is always specially characterised by the peculiar arrangement of the anterior and posterior canals, which are greatly arched, and the position of their openings into the sinus superior (canal commissure) is reversed.

In lower types (Swimming Birds) this peculiarity is less marked than in the higher forms, and it would be interesting to ascertain the condition of these parts in the Struthionidæ, as one would expect to find in them important points of connection with Reptiles.

In many Reptiles the free end of the ductus endolymphaticus is situated close under the roof of the skull beneath the parieto-occipital suture, and in the Ascalabota the duct even leaves the cranial capsule, passes back between the muscles of the neck, and in the region of the pectoral arch becomes swollen to form a large folded sac, from which finger-shaped processes extend to the ventral surface of the vertebral column and to the sub-mucous tissue of the pharynx. These processes may also branch out in a labyrinthic manner into the orbit, and they are always filled with a white semi-solid mass of calcareous substance, as in Anura : calcareous matter is present in the ductus endolymphaticus of all Vertebrates, at any rate in the embryo. In Birds, the duct does not pass out of the cranial cavity.

A tympanic membrane is present in Birds and all Reptiles except Hatteria, Snakes, and Amphisbæ-nians; and in the two last-



FIG. 183.—RIGHT MEMBRANOUS LABYRINTH OF *Turdus musicus*, from the inner side. (After G. Retzius.) Letters as before.

mentioned groups the tympanic cavity and Eustachian tube are also wanting. In Crocodiles the tympanic cavity is very complicated, and in them as well as in Birds, the two Eustachian canals open by a single median aperture into the pharynx. The osseo-cartilaginous columella is well developed in the Sauropsida, and is not distinct from the stapedial plate ; in Hatteria it is continuous distally with the hyoid (p. 92).

In certain Lizards (*e.g.*, Ascalabota, Monitor), an indication of the development of an external auditory passage is seen, the tympanic membrane being partially covered posteriorly by a small fold of skin, usually enclosing the anterior border of the digastric muscle ; and in Crocodiles there is a definite integumentary valve moved by muscles. In certain Birds also (*e.g.*, Owls), there is a moveable valve.

**Mammals.**—The auditory organ of Mammals reaches a much higher stage of development (Fig. 184), but in Monotremes it shows many points of resemblance to that of Reptiles and Birds.

The cochlea now reaches its highest development, and grows into a long tube which becomes spirally coiled on itself.[1] In this

[1] In Man it forms nearly three coils, and in other Mammals from one and a half (Cetacea) up to as many as four or more. Thus in the Rabbit there are two and a half, in the Ox three and a half, in the Pig almost four, and in the Cat three coils. The cochlea, as well as the sacculus and all parts of the pars superior of the membranous labyrinth, vary considerably both in form and arrangement in the various types.

respect, as well as in the more highly-specialised histological struc-
ture of the cochlea, lies the characteristic peculiarity of the auditory
organ of Mammals. The auditory nerve forms the axis of the spiral.

In consequence of this development of the cochlea, the papilla
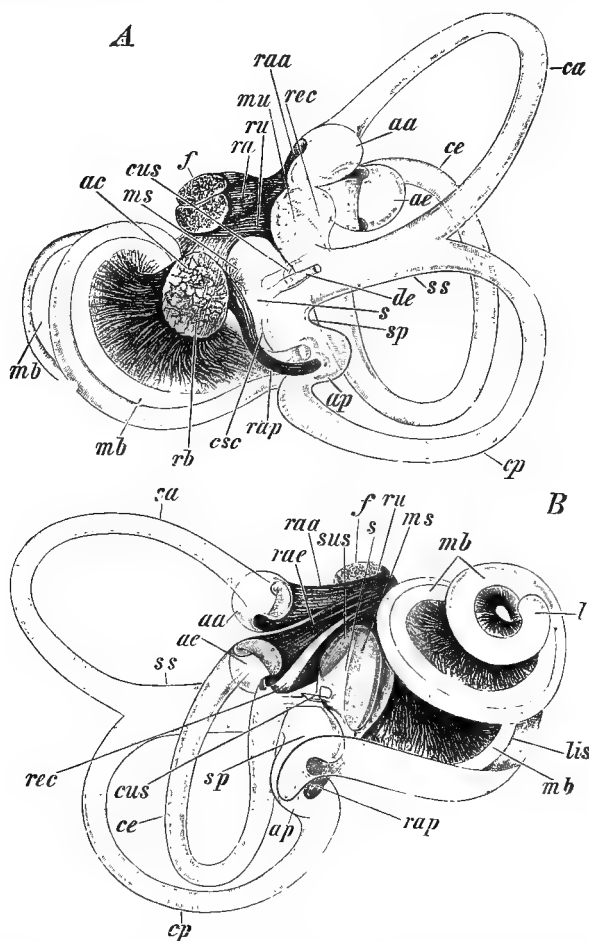


FIG. 184.—RIGHT MEMBRANOUS LABYRINTH OF RABBIT (*Lepus cuniculus*.)
A, from the inner, and B from the outer side.  (After G. Retzius.)

*sus*, sinus utricularis sacculi ; *csc*, canalis reuniens Henseni ; *rb*, basilar branch of
the auditory nerve (*ac*) ; *f*, facial nerve ; *mb*, basilar membrane ; *lis*, spiral
ligament.   (Other letters as Figs. 180–183.)

acustica, or, as it is called in Mammals, the *organ of Corti*, is drawn
out to a considerable length, and the part of the wall of the cochlea
on which it lies is called the basilar membrane, while the opposite
wall is spoken of as the *membrane of Reissner* (Fig. 186) : this is
already represented in Crocodiles and Birds.

The aperture of communication between the pars superior and pars inferior of the membranous labyrinth—that is, between the sacculus and utriculus, is entirely obliterated in Mammals, the two parts being only indirectly connected with one another by means of the ductus endolymphaticus. This bifurcates at its point of insertion into the membranous labyrinth, one limb being connected with the utriculus and the other with the sacculus (Fig. 179); while its upper end perforates the inner wall of the cartilaginous or bony auditory capsule, passes into the cranial cavity, and terminates by an expanded extremity (saccus endolymphaticus) in the dura mater. Osmosis can thus occur between the lymph contained in the endolymphatic and epicerebral lymph-spaces respectively.

The tympanic membrane is secondarily situated deep down in the external auditory meatus, and thus an important difference is seen between the Amphibia and Sauropsida on the one hand, and the Mammalia on the other. The tympanic cavity and Eustachian tube are well developed, and in place of the single bony columella of the Sauropsida there is a chain of three *auditory ossicles*, articulating with one another and extending between the tympanic membrane and the fenestra ovalis. These are—the *malleus*, the *incus* with its orbicular apophysis, and the *stapes*.[1]

The *stapedius muscle* arises from the wall of the tympanic cavity, and is inserted into the stapes, serving to keep the membrane of the fenestra ovalis stretched. It is supplied by the facial nerve and corresponds to a specialised portion of the hinder belly of the biventer, and can be traced back as far as Fishes. A *tensor tympani* supplied by the mandibular division of the trigeminal and derived from the internal pterygoid muscle (primarily from the masticatory muscles of Fishes) also arises from the wall of the tympanic cavity, and is inserted into the manubrium of the malleus, serving to keep the tympanic membrane stretched. Both these muscles are composed of striated fibres.

As already mentioned, the form of the membranous labyrinth is repeated by its enclosing cartilaginous or bony capsule, which forms, so to speak, a sort of cast around its individual parts. Thus it is usual to speak of a cartilaginous or bony labyrinth as distinguished from the membranous labyrinth enclosed within it, the two being separated by the perilymphatic cavity. In Mammals the skeletal labyrinth becomes ossified before any other part of the skull, and is incompletely divided into two parts enclosing the utriculus and sacculus respectively. With the latter part is connected the *bony cochlea*, the axis of which lessens in size from base to apex (Fig. 185), and round it a bony lamella (lamina spiralis ossea) winds in a spiral manner; this extends into the cavity of the coils of the cochlea without quite reaching the opposite wall (Figs. 185 and 186), being continued outwards by two laterally-diverging lamellæ, mentioned above as the basilar

[1] Cp. p. 100 and Figs. 80 and 233, in which the mode of development of these parts is shown. There is often also a bony (interhyal) rudiment in the tendon of the stapedius muscle.

membrane and membrane of Reissner; these lie at an angle to one another and correspond to the inner walls of the membranous cochlea or *scala media*, which is approximately triangular in transverse section. The outer wall abuts against a portion of the peripheral part of the bony cochlea (the region between $Ls$ and the peripheral end of $R$ in Fig. 186). It is apparent therefore that
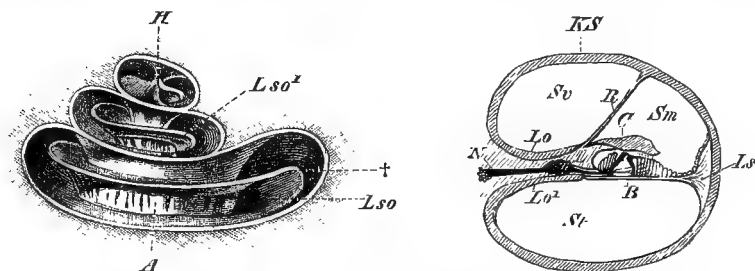


FIG. 185.—BONY COCHLEA OF MAN. (After A. Ecker.)

$A$, axis ; $Lso$, $Lso^1$, lamina spiralis ossea, the free edge of which, perforated by the fibres of the auditory nerve, is visible at † ; $H$, hamulus.

FIG. 186.—DIAGRAMMATIC TRANSVERSE SECTION OF THE COCHLEA OF A MAMMAL.

$KS$, bony cochlea ; $Lo$, $Lo^1$, the two layers of the lamina spiralis ossea, between which at $N$ the auditory nerve (together with the ganglion, left of $L$) is seen ; $L$, limbus laminæ spiralis ; $B$, membrana basilaris, on which the neuro-epithelium lies ; $R$, Reissner's membrane ; $Sv$, scala vestibula ; $St$, scala tympani ; $Sm$, scala media (membranous cochlea) ; $C$, membrane of Corti ; $Ls$, ligamentum spirale.

the scala media does not by any means fill up the lumen of the bony cochlea, but that a cavity is left on either side of it, corresponding to those we have already met with in the auditory organ of Birds and known as the *scala vestibuli* and *scala tympani* (Figs. 179 and 186).

Both of these are continuous with the perilymphatic cavity, and, following the direction of the scala media, open into one another at the blind end of the latter (Fig. 179). The scala vestibuli is shut off from the tympanic cavity by the membrane of the fenestra ovalis, to which the stapes is applied externally ; the scala tympani is closed by the membrane of the fenestra rotunda.

On the floor of the bony cochlea, not far from the fenestra rotunda, is an opening leading into a narrow canal, the *ductus perilymphaticus*, which serves as a communication between the perilymphatic cavity and the peripheral lymphatic trunks of the head (Fig. 179).[1]

The fibres of the auditory nerve running along the axis of the bony cochlea extend in their course laterally outwards, between the two plates

[1] A ductus perilymphaticus can be plainly made out from Reptiles onwards.

of the lamina spiralis ossea (Figs. 186, 187). On the free border of the latter they pass out, and break up into terminal fibrillæ on the inner surface of the basilar membrane.

The fibrillæ extend to the sensory or auditory cells, and these are stretched as in a frame between the firm supporting and isolating cells or bacilli. From the surface of the bacilli a resistant net-like membrane (membrana reticularis) extends laterally, and through the meshes of the latter the hairs of the auditory cells project. The number of the outer hair-cells may be estimated at about 12,000. The auditory cells are covered by a thick and
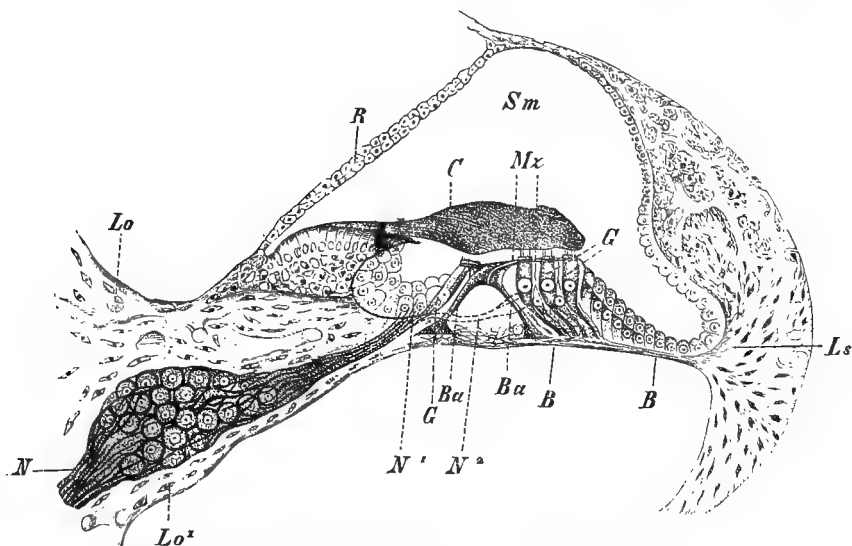


FIG. 187.—THE ORGAN OF CORTI. (After Lavdowsky.)

Lo, Lo¹, the two plates of the lamina spiralis ossea ; N, auditory nerve with ganglion ; N¹, N², the nerve branching up into fibrillæ and passing to the auditory cells (G, G) ; Ba, Ba, bacilli, or supporting cells ; Mx, membrana reticularis ; C, membrane of Corti ; Ls, ligamentum spirale, passing into the basilar membrane ; Sm, scala media ; R, membrane of Reissner ; B, B, basilar membrane.

firm membrane—the membrana tectoria s. Corti —which perhaps acts as a damper, and which arises from the labium vestibulare of the lamina spiralis ossea. The whole extent of the basilar membrane consists of clear thread-like and very elastic fibres, of which about 16,000 to 20,000 can be made out in Man.

A true *pinna* or *auricula* (Fig. 188), attached to the border of the external auditory meatus and projecting freely from the head, occurs in Mammals only (comp. p. 229). It is supported by cartilage, and the intrinsic and extrinsic muscles in connection with it are supplied by the facial nerve.

The pinna arises from a series of rounded eminences on the first and second visceral arches, around the hyoid (spiracular) cleft, the lower part of which closes up, while the upper part gives rise to the external

auditory meatus. These auricular eminences unite to form a nearly continuous ring, on which are later formed the characteristic protuberances known as the *helix*, *antihelix*, *tragus*, and *antitragus*. The variations in the form of the pinna which are seen in various Mammals concern essentially the later formed portion which projects upwards and backwards from the head (Fig. 188).
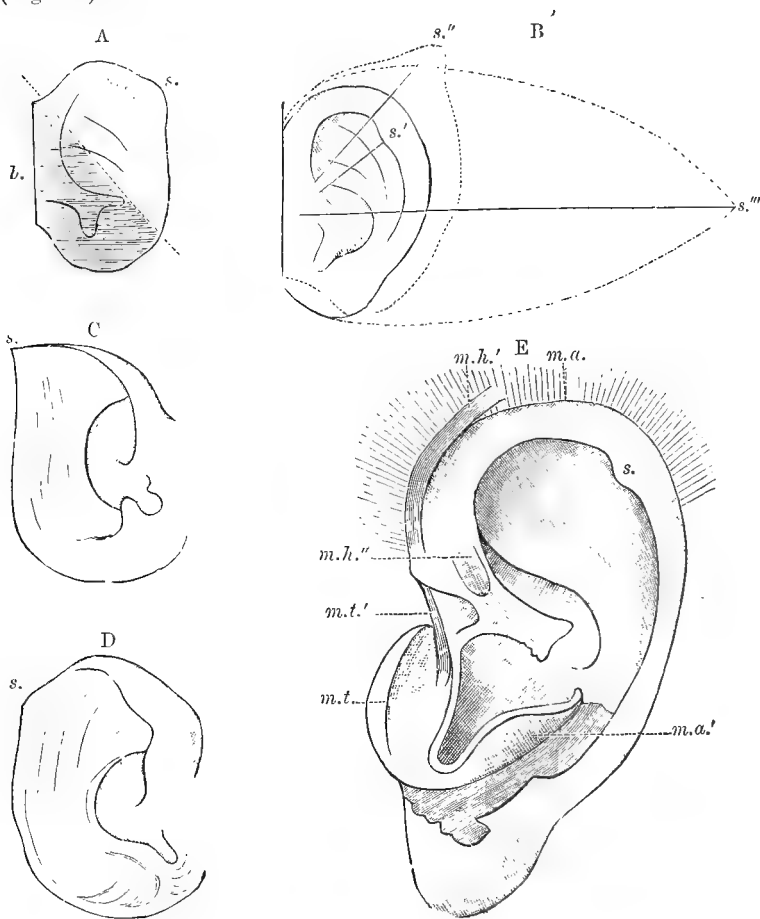


FIG. 188.—THE PINNA OF VARIOUS PRIMATES.

In A, the shaded portion (*b*) represents the zone of the auditory eminences of the embryo, the unshaded that of the later formed auditory fold. B, Man, Baboon and Ox, drawn to the same scale and superposed : *s'*, *s,"* *s*, spina or tip of the ear. C, Macacus rhesus, with upwardly directed tip ; and D, Cercopithecus, with backwardly directed tip. E, Man : the muscles are indicated as follows—*m.a*, attolens auriculæ ; *m.a'*, antitragicus ; *m.t*, tragicus ; *m.t'*, inconstant muscle, extending from the tragicus to the margin of the helix ; *m.h'*, helicis major ; *m.h"* helicis minor ; *s*, tip of the ear rolled over. A-D, after Schwalbe ; E after Henle.

## F. ORGANS OF NUTRITION.

### ALIMENTARY CANAL AND ITS APPENDAGES.

The alimentary canal consists of a tube which begins at the aperture of the *mouth*, passes through the body cavity (cœlome), and ends at the *vent* or *anus*.[1]   Its walls consist of several layers (Fig 214,), of which the *mucous membrane*, lining the cavity of the tube, and the *muscular layer* external to this, extend throughout the canal.   The mucous membrane consists of a superficial *epithelium* and a deeper *connective-tissue layer*, the outer part of which, or *sub-mucosa*, forms a loose network extending to the muscular layer.   The epithelium is derived from the hypoblast, with the exception of that lining the mouth and anus (*stomodæum* and *proctodæum*[2]) which is epiblastic in origin (p. 5).   The connective tissue and muscular layers arise from the splanchnic layer of mesoblast of the embryo ; and the muscular coat, consisting almost entirely of unstriated fibres, supplied with nerves from the sympathetic system, is, as a rule, divided into two layers, the inner being constituted by circular, and the outer by longitudinal fibres. These serve for the contraction or peristalsis of the wall of the gut, and thus fulfil the double function of bringing the nutritive contents of the latter into the closest possible relation with the whole epithelial surface, and at the same time of removing from the body the substances which have not been absorbed.   Striated (voluntary) muscular fibres, supplied by cerebral or spinal nerves, occur only at the anterior and posterior ends of the canal.

An outer accessory *serous* coat, the *peritoneum*, encloses the gut externally in the region of the cœlome.   This is covered on its

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[1] In embryos of many Vertebrates (*e.g.*, Elasmobranchii, Amphibia), a pigmented ridge of cells is formed on the dorsal side of the gut in the head and trunk, and gives rise to a rod lying close beneath the notochord.   In certain cases it remains for a time in connection with the gut by a series of segmental canals which later disappear.   The meaning and subsequent fate of this *sub-notochordal rod* or *hypochorda* are not known.

[2] Phylogenetically the proctodæum is older than the stomodæum, and in many Vertebrates it is derived directly from the blastopore.

free surface by pavement epithelium, and, dorsally to the alimentary
canal, is reflected round the entire body-cavity, converting the
latter into a large lymph-sinus. A *parietal layer*, lining the body-
cavity, and a *visceral layer*, reflected over the viscera, can thus be
distinguished in the peritoneum (Fig. 7). The part where one
passes into the other, which is thus primitively double, is called
the *mesentery*,[1] and this serves not only to support the alimentary
canal from the dorsal body-wall, but also to conduct the vessels
and nerves passing from the region of the vertebral column to the
viscera. With the lengthening of the alimentary canal during
development, the mesentery may give rise to a more or less com-
plicated system of folds in which the viscera are enveloped.

The most anterior section of the primitive alimentary tract
of the Ichthyopsida functions as a *respiratory cavity* as well as a
*food-passage*. A row of sac-like outgrowths, lying one behind the
other, are developed from the mucous membrane and eventually
unite with the ectoderm, apertures being formed to the exterior
(Fig. 189, A). Between the channels thus formed, the visceral
arches (p. 69) are situated, and along the latter certain vessels
are formed by means of which a continual interchange of gases can
take place between the blood and the air contained in the water
passing through the sacs. In this manner the *gills* or *branchiæ*
(p. 273) arise. Even in the Amniota, although gills are not
developed, the larger portion of the cavities of the mouth and
pharynx lying behind the internal nostrils serves as a common air-
and food-passage until a proper palate (pp. 92, 202) is formed (Fig.
189, C).

With the formation of a definite palate (most Amniota), the
primitive mouth-cavity becomes divided into an upper *respiratory*,
and a lower *nutritive portion*—that is, into a *nasal* and a *secondary*
or *definitive mouth-cavity*. The separation, however, is not a com-
plete one, the passage being common to both cavities for a certain
region (Fig. 189, D). This region, in all Vertebrates, is called
the *pharynx*, and in Mammals it is partially separated from the
mouth by a fibrous and muscular fold, the *velum palati*, or free
edge of the *soft palate*.[2]

The alimentary canal of Vertebrates is typically divisible into
the following principal sections (Fig. 190):—*Mouth* or *oral
cavity, pharynx, gullet* or *œsophagus, stomach, small intestine*, and
*large intestine*. The large intestine may communicate with a
*cloaca*, into which the urinary and genital ducts also open, or it
may open directly to the exterior. The small intestine may be
further differentiated into *duodenum, jejunum* and *ileum*, and the
large intestine into *colon* and *rectum*. A blind-gut or *cæcum* is

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[1] In Murænoids, Dipnoans, and Lepidosteus, a *ventral mesentery* is also present,
but in Lepidosteus it only extends for a short distance along the hinder part of
the gut.
[2] A membranous velum palati exists in Crocodiles.
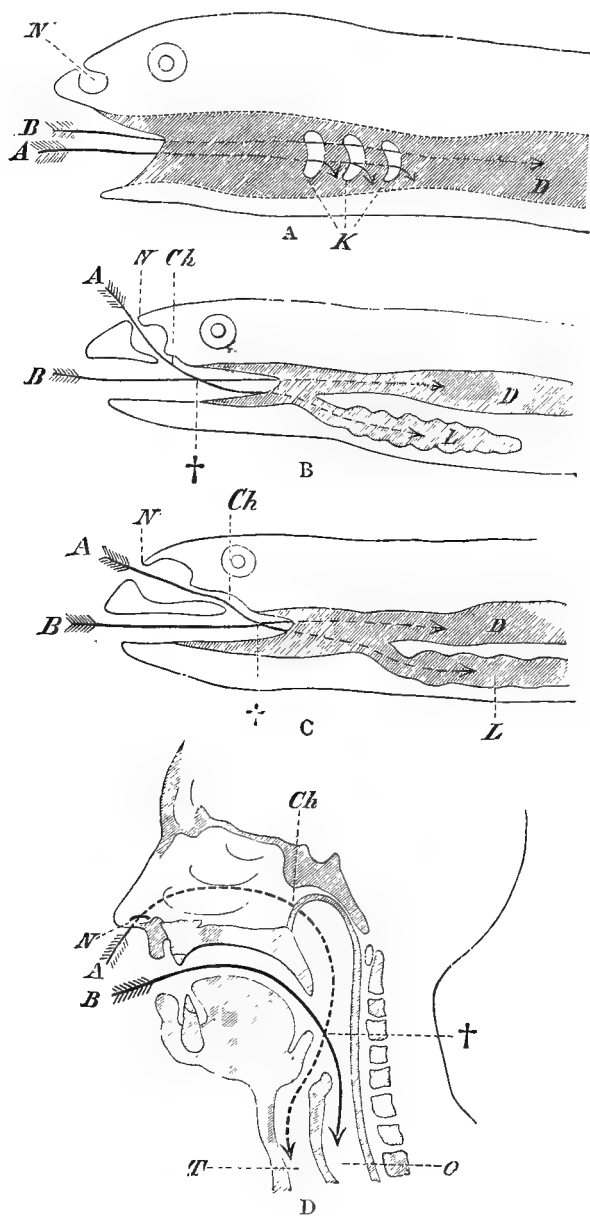
FIG. 189.—DIAGRAMS OF THE ORAL CAVITY AND PHARYNX OF A FISH (A),
AMPHIBIAN (B), REPTILE OR BIRD (C), AND MAN (D).

*N*, external nostril; *Ch*, internal nostril; *D*, alimentary canal; *K*, gill-slits;
*L*, lung; *T*, trachea; *O*, œsophagus: the arrow marked *A* indicates the
respiratory passage, that marked *B* the nutritive passage; |, the point where
the two passages cross one another.

often present at the junction of the large and small intestine.
Between the stomach and duodenum as well as between the ileum
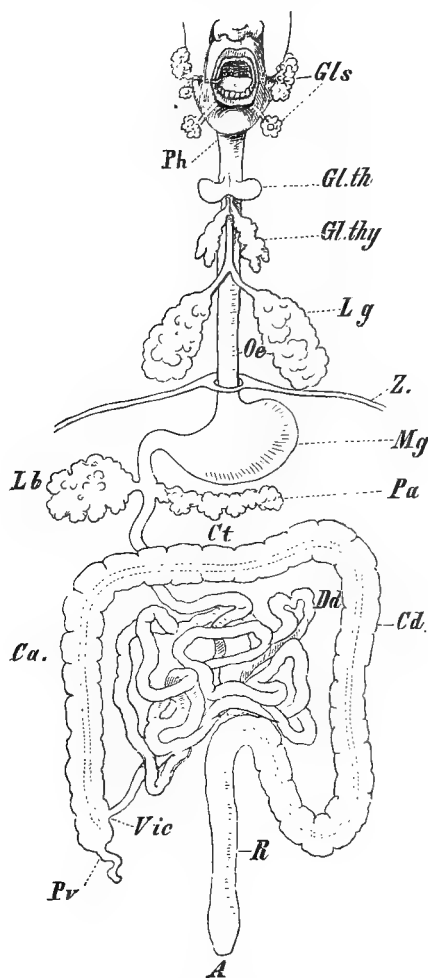


FIG. 190.—DIAGRAM OF THE ALIMENTARY CANAL OF MAN.

*Gls*, salivary glands ; *Ph*, pharynx ; *Gl.th*, thyroid ; *Gl.thy*, thymus ; *Lg*, lung ;
   *Oe*, œsophagus ; *Z*, diaphragm ; *Mg*, stomach ; *Lb*, liver ; *Pa*, pancreas ;
   *Dd*, small intestine ; *Vic*, ileo-colic valve ; *Pv*, vermiform appendix (cæcum) ;
   *Ca*, *Ct*, *Cd*, ascending, transverse, and descending portions of the colon ; *R*,
   rectum ; *A*, anus.

and large intestine there is, as a rule, a marked elevation of the
muscular coat serving as a sphincter (*pyloric* and *ileo-colic valves*).
There is also a sphincter muscle at the anus.

The small intestine is in most cases the longest section of the alimentary tract : the bile and pancreatic ducts open into its anterior portion.

In almost all cases the alimentary canal becomes more or less coiled, and thus presents a greater surface for absorption. As a general rule, it is relatively longer in herbivorous than in carnivorous animals. A considerable increase of surface also commonly results from the elevation of the mucous membrane to form folds, villi, and papillæ (p. 269).

Certain *appendages* are present in connection with the alimentary canal. These are all developed primarily from the hypoblast and are thus of epithelial origin : mesoblastic elements are added to them secondarily. Whether they function as glands throughout life or not, they are all formed on the same type as glands.

Beginning from the mouth the following appendicular organs may be distinguished (Fig. 190) :—

(1) *Mucous and salivary glands.*
(2) The *thyroid.*
(3) The *thymus.*
(4) The *lungs* or *air-bladder.*
(5) The *liver.*
(6) The *pancreas.*

In addition to these, *gastric* and *intestinal glands* are embedded in the wall of the gut.

## MOUTH.

In Amphioxus the entrance to the mouth (oral hood) is provided with cirrhi, and in Petromyzon[1] it is surrounded by a ring of cartilage (Fig. 54) : all other Vertebrates are provided with *jaws.*

Definite *lips* provided with muscles first appear in Mammals, but are wanting in Monotremes. The space between them and the jaws is spoken of as the *vestibulum oris;* this may become extended on either side to form *check-pouches,* which serve as food reservoirs (many Monkeys and Rodents).

The chief organs of the oral cavity are the *teeth,* the *glands,* and the *tongue.*

## Teeth.

The teeth are developed quite independently of the endoskeleton, and both epiblast and mesoblast take part in their formation (comp. p. 30). The first traces of the teeth are seen primarily

[1] The mouth of the Lamprey serves as a suctorial organ for attaching the animal to foreign objects. The larvæ of Lepidosteus and Anura are temporarily provided with suctorial organs

in the form of superficial papillæ of the mucous membrane; but secondarily, owing to want of space, the epithelium of the mouth grows inwards so as to give rise to a *dental lamina* which becomes enlarged distally at certain points to form the so-called *enamel-organs*. These as they grow deeper into the mesoblast become bell-shaped, and enclose modified masses of connective-tissue, the *dental papillæ*; the upper cells of the papillæ, *i.e.*, those next to the enamel-organ are known as *odontoblasts* (Fig. 191, A). The epithelial and connective tissue germs come into the closest relation with one another
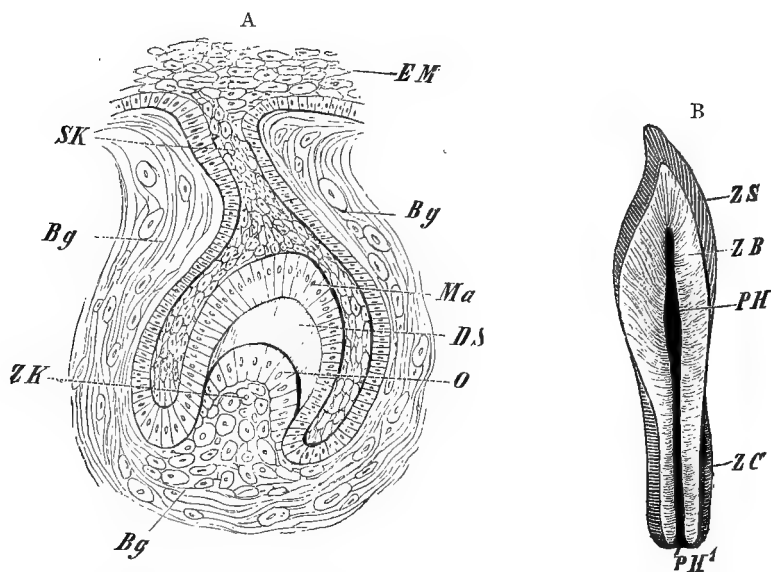


Fig. 191A.—Diagram of the Development of a Tooth.

*EM*, epithelium of mouth; *SK*, dental lamina; *ZK*, dental papilla; *Ma*, membrana adamantina of enamel-organ; *O*, odontoblasts; *DS*, dentine; *Bg*, *Bg*, connective tissue follicle or sac surrounding the tooth.

Fig. 191b.—Semidiagrammatic Figure of a Longitudinal Section through a Tooth.

*ZS*, enamel; *ZB*, dentine; *ZC*, cement; *PA¹*, aperture of the pulp-cavity (*PH*).

and give rise respectively to the calcified *enamel* and *dentine* (ivory), of which the teeth are composed. The enamel is the harder and contains little organic matter, and the dentine is permeated by a system of fine canals in which are delicate processes of the odontoblasts. A third, bone-like substance, the *cement*, is also formed round the bases of the teeth, and between the folds of enamel when these are present; it may unite with the bones of the jaw. The root of the tooth, embedded in the gums, is provided at its

lower end with an opening leading into the central *pulp-cavity* (Fig. 191, B), into which blood-vessels and nerves extend.

In most Vertebrates below Mammals all the teeth are essentially similar in form (*homodont dentition*): in Mammals, on the other hand, they become differentiated into distinct groups (*heterodont dentition*), known as *incisors*, *canines*, and *cheek-teeth* or *grinders* (*premolars* and *molars*).

A succession of teeth takes place throughout life in almost all Vertebrates except Mammals, in which there are very exceptionally more than two functional sets, the so-called *milk-* or *deciduous teeth* and the *successional teeth*. This difference is expressed by the terms *polyphyodont* and *diphyodont*. (Comp. p. 245).

**Fishes, Dipnoans, and Amphibians.**—The homology and similarity of the teeth with the dermal denticles of Elasmobranchs has already been treated of (p. 30). The most primitive form of the tooth is that of a simple cone, but even amongst Elasmobranchs, in which the teeth are arranged in numerous parallel rows upon the cartilaginous jaws, this form has already become modified in various ways for seizing or crushing the food.

Of those Anamnia which possess a bony skull, four groups of tooth-bearing bones may in general be distinguished, viz., (1) the maxillary arch (*premaxilla* and *maxilla*); (2) the palatal arch (*vomer*, *palatine*, *pterygoid*); (3) the (unpaired) *parasphenoid*; and (4) the mandibular arch (*dentary* and *splenial*).[1]

True teeth are wanting in Cyclostomes, and amongst cartilaginous Ganoids they are absent in the adult Sturgeon, though rudiments are present in the embryo. Amongst Teleostei they are wanting in the



FIG. 192.—SKULL OF *Batrachoseps attenuatus*. (From the ventral side, showing the teeth on the parasphenoid.)

adult Lophobranchii and in Coregonus. In the Cyclostomes they are represented functionally by a number of conical *horny* teeth.[2]

In bony Ganoids and Teleosts, teeth may be present on all the bones bounding the oral cavity, as well as on the hyoid and the branchial arches (" pharyngeal bones "). In the latter position, as well as on the parasphenoid, they often form brush-like groups. In form the teeth may be cylindrical, conical, or hooked; or they may be chisel-shaped (Scarus, Sarginæ),

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[1] The teeth of Elasmobranchs may be compared to (2) and (4) of these.

[2] Structures bearing a superficial resemblance to vestigial true teeth are recognisable beneath the horny teeth, but they possess no odontoblasts or enamel epithelium.
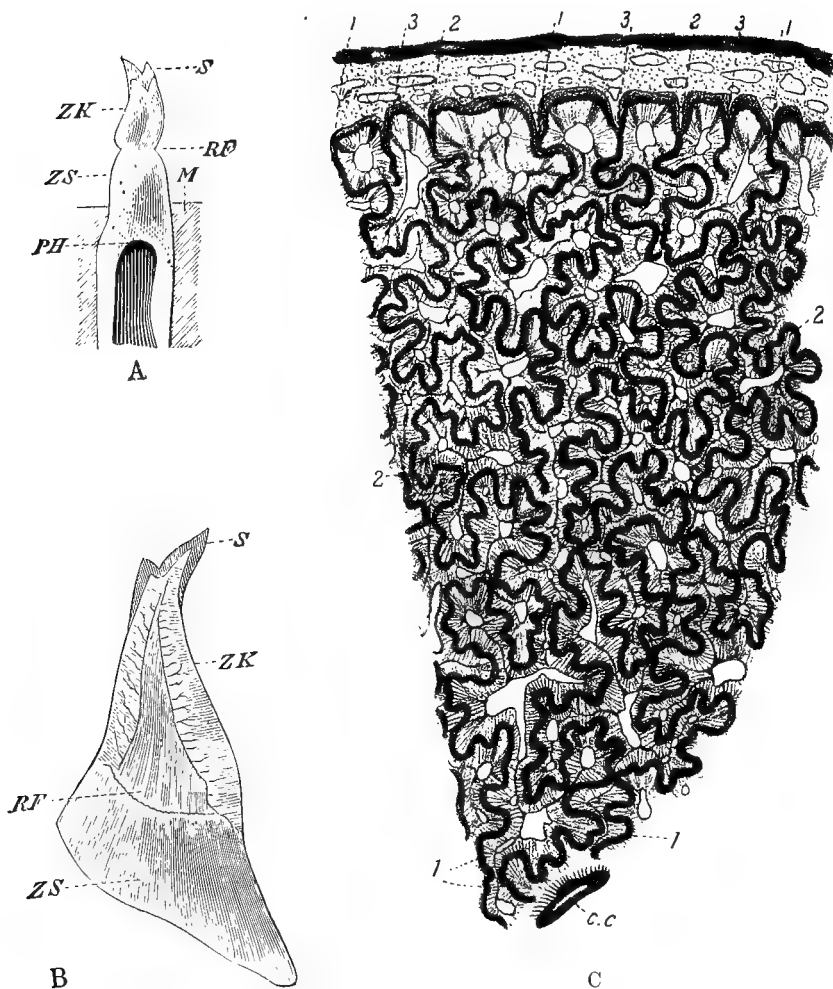
FIG. 193, A.—TOOTH OF FROG, AND 193, B, *Salamandra atra.*

ZK, crown; ZS, base; RF, circular furrow; S, apex, covered with enamel;
PH, pulp-cavity; M, maxilla.

FIG. 193, C.—TRANSVERSE SECTION THROUGH PORTION OF A TOOTH OF A LABY-
RINTHODONT (*Mastodonsaurus*).    (After J. Storrie.)

C.c, central pulp-cavity; 1, inflections of the enamel, surrounded by dentine,
which reach the centre (c.c); 2, half-length inflections between 1; 3, short
inflections between 1 and 2.

resembling the incisors of Mammals, and working together like
scissors; in some Fishes they give rise to a definite pavement,
are rounded in form, and serve to crush the food.    They may,

again, be delicate and bristle-like (Chætodon), or sabre-shaped (Chauliodus).

In the Dipnoi (Fig. 62) the teeth are compound and exceedingly massive, presenting sharp edges and points.

In the Amphibia there is in general a considerable diminution in the number of teeth as compared with Fishes ; and at the same time a much more uniform character is noticeable in their form throughout (Fig. 193, A, B). They are enlarged conically below, and rest on a definite base, while above they become narrower and slightly curved, ending either in a double (Myctodera, Anura), or a single apex (Perennibranchiata, Derotremata, Gymnophiona); the latter is the more primitive condition. The teeth lie deeply embedded in the mucous membrane, and are present, as a rule, on the premaxilla, maxilla, and mandible (except in Anura), as well as on the vomer and palatine, but rarely on the parasphenoid (certain Urodeles, Fig. 192) ; in the larvæ of Salamanders and in Proteus the splenial of the lower jaw is also toothed. *Horny teeth* and *horny jaws*, developed entirely from the epidermis, are present in larval Anura, and similar structures occur in Siren lacertina.

Teeth are altogether absent in the Bufonidæ and in Pipa.

The teeth of certain of the Stegocephala (Labyrinthodonta) were extremely complicated, the enamel appearing as numerous corrugated folds extending from the periphery towards the centre (Fig. 193, C).

**Reptiles and Birds**.—Corresponding with the greater firmness of the skull in Reptiles, the dentition is usually strongly developed, and occasionally at the same time it is more highly differentiated than in Amphibians. The teeth are either situated upon a ledge on the inner side of the lower jaw, with which they become fused basally (*pleurodont* dentition—most Lacertilia) ; or they lie on the free upper border of the jaw (*acrodont* dentition—Chameleon) ; or finally ,as in Crocodiles and numerous fossil Reptiles, they are lodged in alveoli (*thecodont* dentition) (Fig. 194, A, *a*, *b*, *c*). Both upper and lower jaws, and occasionally the palatine and pterygoid also, are toothed (Lizards and Snakes) ; and in Hatteria, vomerine teeth may also be present. The teeth are usually conical and more or less pointed, but in Lizards the apex is double, and in many Reptiles (*e.g.*, Palæohatteria, Hatteria, Uromastix spinipes, Agamæ, and numerous fossil forms, especially the Theriodontia of the Trias of South Africa), a heterodont dentition is already indicated. Almost all Reptiles are polyphyodont.

In poisonous Snakes a varying number of maxillary teeth are differentiated to form *poison-fangs*. Thus in the common Viper (Pelias berus) there are on each side ten poison-fangs arranged in transverse rows ; the stronger ones project freely, while the lesser, reserve teeth lie within the gum (Fig. 195, A) ; only one of these teeth, however, is firmly fixed to the maxilla at a time. Each fang

is perforated by a poison-canal, which is incompletely surrounded by the pulp-cavity, the latter having the form of a half-ring in
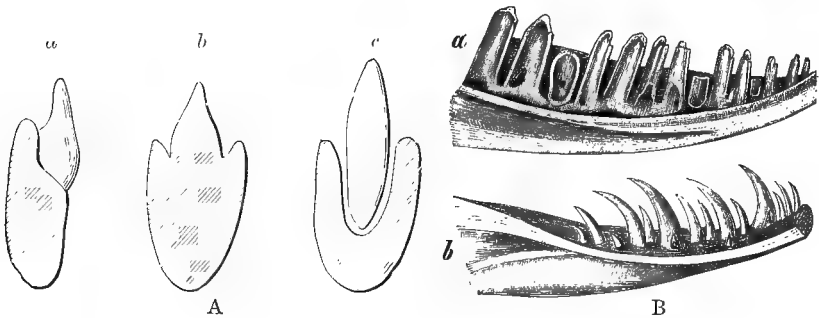


FIG. 194.—A, DIAGRAMS OF TRANSVERSE SECTION THROUGH THE JAWS OF REPTILES, SHOWING PLEURODONT (*a*), ACRODONT (*b*), AND THECODONT (*c*) DENTITIONS. B, *a*, LOWER JAW OF *Zootoca vivipara* ; *b*, OF *Anguis fragilis*. (After Leydig.)

transverse section (Fig. 195, B, C,) : the duct of the poison-gland passes into an aperture at the base of the tooth which leads into.
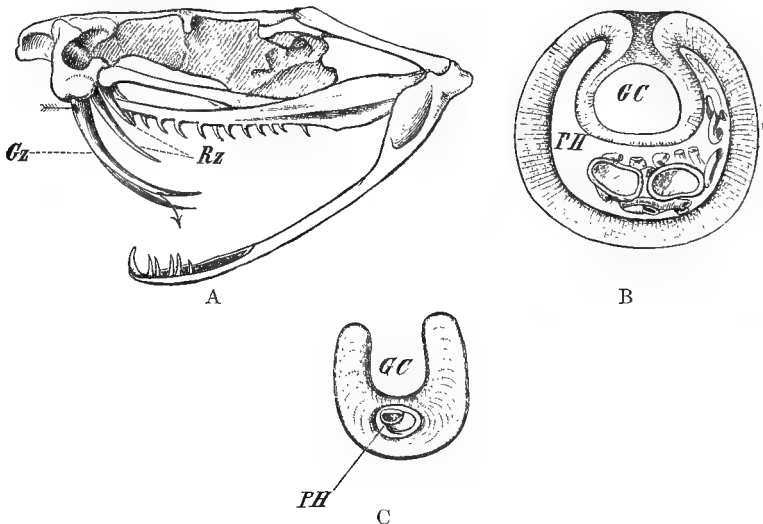


FIG. 195.—FIGURES OF THE POISON-FANGS OF A VIPERINE SNAKE.

*A*, skull of Rattlesnake ; B, transverse section through about the middle of the poison-fang of *Vipera ammodytes* ; C, transverse section through the poison-fang of *Vipera ammodytes* near its distal end. (B and C after Leydig.) *Gz*, poison-fang ; *Rz*, reserve fangs ; *GC*, poison-canal ; *PH*, pulp-cavity.

the poison-canal, and the latter opens at a short distance from the apex of the tooth (see the course of the arrow in Fig. 195, A).

Between the ordinary teeth of Snakes and the poison-fangs with closed canals, there are numerous intermediate forms in which certain of the teeth are simply grooved along their anterior side. A similar condition is also seen in the teeth of the lower jaw of a poisonous Mexican Lizard (Heloderma). (Comp. p. 252.)

A peculiar tooth is present in the embryos of Lizards and some Snakes. It projects considerably beyond its neighbours, and lies in the median line of the lower jaw, extending vertically towards the snout and serving the young as a means of breaking through the parchment-like egg-shell. This must not be confounded with the horny "neb" in Crocodiles, Chelonians, Birds, and Monotremes amongst Mammals, which is of a purely epithelial nature.

Chelonians, like existing Birds, are provided with horny sheaths to the jaws instead of teeth. The presence of teeth in the embryo of Trionyx, as well as of a rudimentary dental lamina in embryos of Chelone and Sterna, for example, proves, however, that this is only a secondary condition.

In the cretaceous Birds of N. America (*Odontornithes*) teeth were present, and were either situated in a definite alveoli (Ichthyornis), or simply in grooves (Hesperornis). The premaxillæ were toothless, and seem to have possessed a horny beak. The single-pointed, smooth teeth of Archæopteryx were probably situated in alveoli. It is possible that some of the Eocene Birds (*e.g.*, Argillornis, Gastornis) possessed teeth.

**Mammals.**—The heterodont dentition characteristic of the Mammalia as a Class must have arisen by a modification of a simple homodont condition, in which the teeth were all conical and of similar size and shape. Side by side with this modification, a shortening of the jaws has usually taken place, and the teeth serve not only to seize and bite the food, but also to masticate it and to test its qualities. The frequent presence of rudimentary, functionless teeth, renders it probable that in the course of phylogenetic development the teeth have undergone a decrease in number.[1] An increase in number, such as is met with in toothed Whales, is due to the separation, during ontogeny, of the component cusps of complex teeth, and is therefore not a primitive, but a highly specialised condition.

As already mentioned, the succession is nearly always reduced to two functional sets, the so-called *milk* or *deciduous teeth* and the *successional* or *permanent teeth*, and in some cases (see p. 249) even one of these may be rudimentary. Traces, however, of an earlier set occur in certain Mammals : this may be spoken of as a "premilk dentition." Occasionally also (*e.g.*, in Man) one or more teeth appear which replace the corresponding "permanent" teeth and thus indications of four—and possibly even of five—sets can in all be recognised.

In each of the two functional sets, *incisors, canines,* and *cheek-*

[1] The last molar of Man, or so-called "wisdom-tooth," seems to be gradually disappearing ; it appears last and is lost first, and often does not reach the grinding surface. In many cases also the outer upper incisors are wanting.

*teeth,* or *grinders,* can as a general rule be distinguished. The teeth which replace the milk-grinders are distinguished as *premolars* from the *molars,* which are situated further back in the jaw and have no predecessors.[1]

All the teeth are imbedded in well-developed alveoli of the jaw-bones, the upper incisors being situated in the premaxillæ, the upper canines and cheek-teeth in the maxillæ, and the lower teeth in the mandible (dentary). The canine, which corresponds to a specially differentiated premolar, and is most characteristically developed in Carnivora, lies in a more or less continuous series with the incisors. The premolars follow behind the canine, the space usually present between them being called the *diastema,* and then come the molars. The primary arrangement of the teeth is such that there is an alternation between those of the upper and lower jaw : thus the teeth in one jaw do not usually correspond in position with those of the other, but with the interspaces between them.

In some cases the enamel-organ persists in all the teeth, which then continue to grow throughout life (*e.g.,* Lepus); in others this is true of the incisors only (*e.g.,* numerous Rodents, Elephant); but more usually growth ceases after a certain time, and the teeth then form definite *fangs* or *roots,* each perforated by a small canal communicating with the reduced pulp-cavity.

The incisors are usually chisel-shaped, while the canines, in those cases where they are most characteristically developed (Carnivora), possess a pointed, conical form, and are more or less curved. The cheek-teeth either possess sharp, cutting crowns (*e.g.,* Carnivora), or the crowns are broad and more or less flat and tuberculated, and adapted for grinding the food. In the latter case the relations of the enamel, dentine, and cement are such as to produce an uneven surface with wear, showing a characteristic pattern in the different groups (Figs. 196—200).

The relations and number of the tubercles—which may be conical (*e.g.,* Pig) or crescentic (*e.g.,* Horse, Ruminants, Fig. 199), as well as the form of the teeth in general, is of great importance in elucidating the ancestral history of the Mammalia, and attempts have been made to trace the evolution of the various forms of molar met with in the Class. According to one view the tuberculated molar has arisen by the gradual modification of a single conical tooth, which has produced lateral outgrowths or buds. Thus taking the simple conical form such as exists in toothed Whales as the most primitive form of mammalian tooth, we find that certain extinct Mammals (*e.g.,* Triconodon) possessed teeth with a main cone and two lateral cusps. It has been supposed that the more complicated forms have been derived from this *triconodont* tooth—firstly by a rotation of the lateral cusps outwards in the upper, and inwards in the lower tooth, thus forming a *trituberular* tooth, with three cusps arranged in a triangle ; and secondly by the addition of other cusps, the first to appear being the posterior heel or talon.

Another hypothesis is that the mammalian cheek-teeth were primarily

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[1] It must, however, be remembered that in some cases the so-called premolars have no predecessors (*see* p. 249).
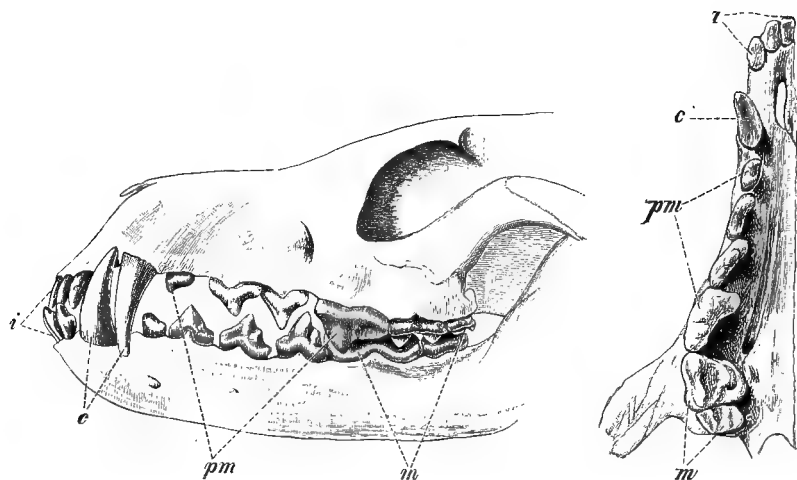
FIG. 196.—DENTITION OF THE DOG (*Canis familiaris*).
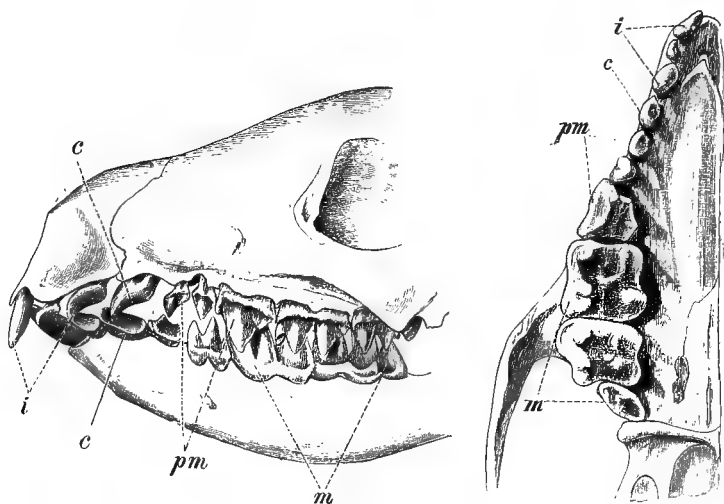


FIG. 197.—DENTITION OF THE HEDGEHOG (*Erinaceus europæus*).
(The teeth of both jaws from the side, and those of the upper jaw from below.)

*i*, incisors ; *c*, canines ; *pm*, premolars ; *m*, molars.

multitubercular, having originated by the fusion of a number of simple coni-
cal teeth ; and certain facts in their development and the presence of multi-
tuberculate Mammals in the Triassic rocks, as well as a comparison with
the massive teeth met with in various Fishes for example, seem to sup-
port this view. The resulting decrease in number is compensated for by the
greater perfection of the individual teeth.
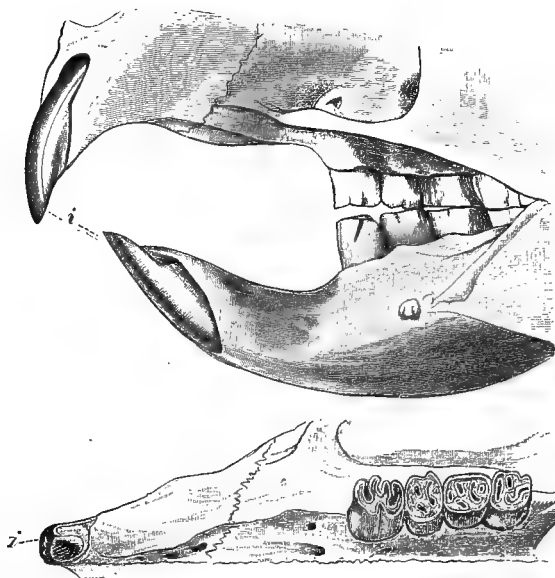
FIG. 198.—DENTITION OF THE PORCUPINE (*Hystrix hirsutirostris*).
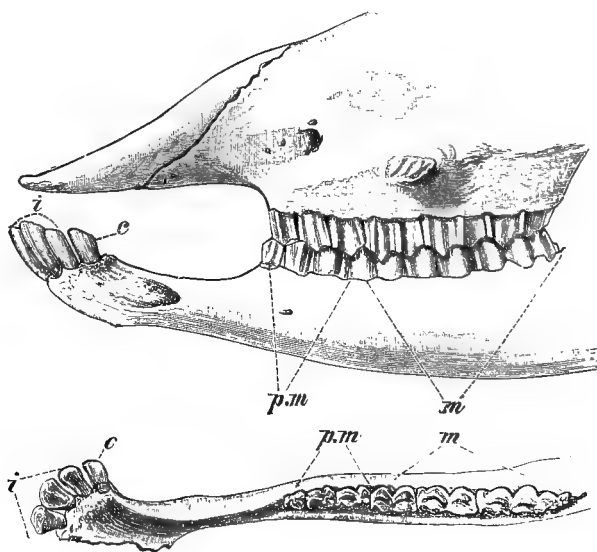


FIG. 199.—DENTITION OF SHEEP (*Ovis aries*).

(References as before, but in Fig. 199 the teeth of the lower instead of the upper jaw are figured from the surface.)

The limitation of the succession to two or even one functional set is probably due to the concentration of several successive generations of teeth in correspondence with the higher development of the individual tooth. This concentration is most marked in Marsupials, in which only a single tooth, usually described as the fourth premolar, has a predecessor. Differences of opinion exist as to whether this tooth is to be regarded as the last remains of the first or of the second set, or whether it belongs to the same series as the others and is only retarded in development. The fact that
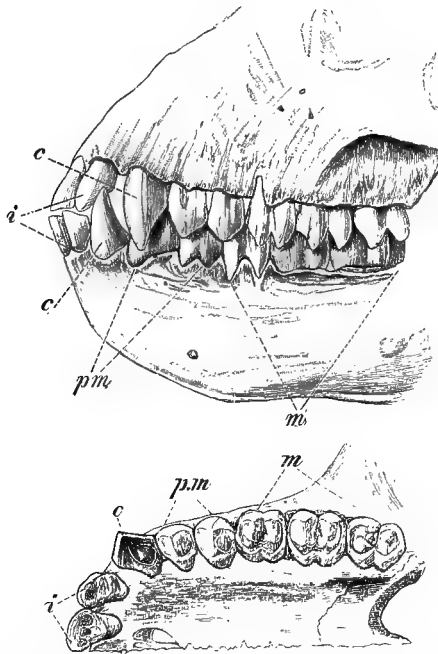


FIG. 200.—DENTITION OF A CATARRHINE MONKEY (*Nasalis larvatus*).

References as before.

in toothed Whales the milk-teeth persist and the second set is only represented in rudiment, seems to indicate that the teeth of Marsupials, except the fourth " premolar " belong to the first set, and that the milk dentition of Mammals is not a secondary acquisition. In other words, the primitive Mammalia were at least diphyodont, and the apparent monophyodont condition seen (*e.g.*, in toothed Whales) is a secondary condition. In the placental Mammals the second dentition becomes of greater importance than the first.[1]

[1] In many instances, however, the first premolar appears to belong to the milk dentition, and this may possibly be the case as regards the molars also.

In describing the teeth of a Mammal it is convenient to make use of a *dental formula* in which their number and arrangement can be seen at a glance, the teeth of one side only being represented. Thus the adult dental formula of those animals, the teeth of which are represented in Figs. 196 to 200, would be—

$$\text{Fig. 196. Dog,} \quad \frac{3 \cdot 1 \cdot 4 \cdot 2}{3 \cdot 1 \cdot 4 \cdot 3} \qquad = 42$$

$$\text{,, 197. Hedgehog,} \quad \frac{3 \cdot 1 \cdot 3 \cdot 3}{2 \cdot 1 \cdot 2 \cdot 3} \qquad = 36$$

$$\text{,, 198. Porcupine,} \quad \frac{1 \cdot 0 \cdot 1 \cdot 3}{1 \cdot 0 \cdot 1 \cdot 3} \qquad = 20$$

$$\text{,, 199. Sheep,} \quad \frac{0 \cdot 0 \cdot 3 \cdot 3}{3 \cdot 1 \cdot 3 \cdot 3} \qquad = 32$$

$$\text{,, 200. Catarrhine Monkey,} \quad \frac{2 \cdot 1 \cdot 2 \cdot 3}{2 \cdot 1 \cdot 2 \cdot 3} = 32$$

The most complete dentition is seen amongst Marsupials, the dental formula of Myrmecobius being $\frac{4 \cdot 1 \cdot 3 \cdot 5 \text{ or } 6}{3 \cdot 1 \cdot 3 \cdot 5 \text{ or } 6} = 50$---$52$. The more typical arrangement is $\frac{3 \cdot 1 \cdot 4 \cdot 3}{3 \cdot 1 \cdot 4 \cdot 3} = 44$.

Sexual differences in dentition exist in a number of Mammals. Thus in the male Wild Boar, Narwhal (Monodon), Dugong (Halicore), and Musk-deer a modification of certain of the teeth (the canines or the incisors) to form *tusks* occurs, and these serve as fighting weapons. In the Elephant and Walrus tusks are present in both sexes : in the former they correspond to incisors, and in the latter to canines.

In Ornithorhynchus the teeth become replaced functionally after a time by the development of horny masticatory plates,[1] and in Echidna they are wanting altogether. Adult Whalebone Whales and certain Edentates (Myrmecophaga, Manis) are toothless, but rudiments of teeth exist in the embryo. In other Edentates the teeth are wanting in enamel. Canines are absent in certain Mammals (*e.g.*, Rodents) and the incisors may also be wanting. In the typical Ruminants incisors and canines are present in the lower jaw only.

### Glands of the Mouth.

The glands of the mouth, like those of the orbit and integument, appear first in terrestrial Vertebrates, that is, from Amphibians onwards. They have the function of keeping moist the mucous membrane which comes into contact with the outer air. From being at first almost entirely unspecialised, and giving rise simply to a slimy fluid, they become differentiated later into structures the secretions of which take on a very important function in relation to digestion ; they may also, as in the case of poisonous Snakes and Lizards, constitute dangerous weapons of offence.

With their gradually increasing physiological importance a

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[1] Horny crushing plates are also present in the Sirenia, the existing forms of which possess numerous teeth, while the extinct Rhytina was toothless.

greater morphological complication both as regards number and arrangement takes place. Their histological character also becomes changed in such a manner that the most varied forms of glands may be recognised.

**Amphibians.**—With the exception of the Perennibranchiata Derotremata, and Gymnophiona, a tubular gland becomes developed in all Amphibia from the anterior portion of the roof of the mouth (comp. Fig. 160), the main mass of which in Urodeles lies in the cavity of the nasal septum or premaxilla (*intermaxillary* or *internasal gland*). In Anura its position is more anterior than in the Urodela, and it is more largely developed; but in both cases the ducts open on to the anterior part of the palate.

In Anura there is a second gland (*pharyngeal gland*) present in the region of the internal nostrils, the secretion of which passes partly into the latter and partly into the pharynx.

Numerous gland-tubes are also present in the tongue of Amphibians, and in the Gymnophiona oral glands are abundant.
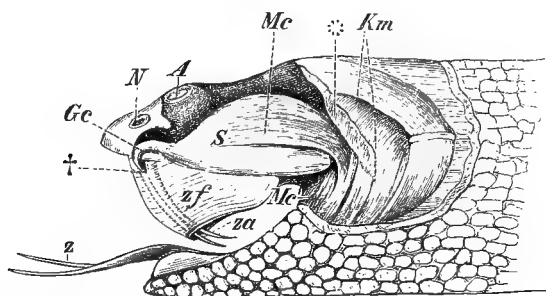


FIG. 201.—THE POISON-APPARATUS OF THE RATTLESNAKE.

*S*, the fibrous poison-sac, which is surrounded by the constrictor-muscle, *Mc* at *Mc¹* an extension of the latter towards the lower jaw can be seen; *Gc*, the duct arising from the poison-gland, which passes into the poison-fang at †; the latter is embedded in a large sac of the mucous membrane, *zf*; *Km*, masticatory muscles, some of which are seen cut through at *; posterior to this the cut edge of the scaly integument is seen; *N*, external nostril; *A*, eye displaced towards the antero-dorsal aspect; *z*, tongue; *za*, aperture of the poison-fang.

**Reptiles.**—The mouth-glands in Reptilia show an advance on those of Amphibia inasmuch as they are separated into groups. Thus not only is there a *palatine gland*, homologous with the intermaxillary gland, but *lingual* and *sublingual*, as well as upper and lower *labial glands* are present. Chameleons and Snakes are distinguished by a remarkable richness in glands, which become most specialised into definite groups in the latter. In poisonous Snakes the *poison-gland* becomes differentiated from a portion of the upper labial gland. It is enclosed in a strong

fibrous sheath, and is acted upon by powerful muscles, so that its secretion can be poured with great force into the duct (Fig. 201), and thence into the poison-fang (p. 243).

The sublingual gland of a Mexican Lizard, Heloderma, has a similar poisonous nature. The secretion passes out through four ducts, which perforate the bones of the lower jaw in front of the grooved teeth (p. 245).

In marine Chelonians and Crocodiles there are no large glands united into groups connected with the mouth.

**Birds.**—In Birds, and more especially in climbing Birds (Scansores), a well-developed lingual gland is present opening on the floor of the mouth, as well as a gland at the angle of the latter. There is no doubt that the lingual glands are homologous with those of Lizards, but it is not known whether the gland at the angle of the mouth corresponds with the posterior upper labial gland of Reptiles—that is to the poison-gland of Snakes. The palatine glands of Birds are not homologous with those of Reptiles and labial glands are wanting.

**Mammals.**—Three sets of salivary glands may be distinguished in connection with the mouth in Mammals, which are called, according to their position, (1) *parotid*, (2) *submaxillary*, and (3) *sublingual*. Each of the two former of these opens into the mouth by a well-defined duct, that of the sublingual having several independent ducts. A special *retrolingual* portion usually becomes differentiated from the sublingual gland and communicates with the submaxillary duct.

The parotid is usually situated at the base of the external ear : its origin is not known. The submaxillary is a compound gland, consisting of glandular elements which differ from one another histologically : it lies beneath the mylohyoid muscle, close to which the retrolingual gland is also situated ; the latter is wanting in only a few Mammals (*e.g.*, Rabbit, Horse). The sublingual gland extends between the tongue and the alveoli of the teeth, and is rarely absent (*e.g.*, Mouse, Mole).

With the exception of the parotid, all these glands, together with certain smaller and less important ones, are homologous with the oral glands of lower Vertebrates.

Salivary glands are wanting in the Cetacea.

## Tongue.

**Fishes.**—The tongue is, as a rule, rudimentary in Fishes, and is simply represented by a fold of mucous membrane covering the basi-hyoid, which in all the higher Vertebrates serves as a point of origin for many of the lingual muscles. Except in Cyclostomes, where it has to do with the suctorial apparatus, the tongue of

Fishes is not capable of movement apart from the visceral skeleton, and is wanting in a proper musculature. It is provided with papillæ and serves only as a tactile organ, or, when provided with teeth (*e.g.*, certain Teleostei, Fig. 60), as a prehensile organ also.

In **Dipnoans** the tongue is not more highly differentiated than in many Fishes.

**Amphibians.**---In the Perennibranchiata (*e.g.*, Proteus) there is a little advance on the condition seen in Fishes, but in all other Amphibia except the Aglossa (Pipa and Xenopus), in which it has become degenerated, the tongue reaches a higher stage, owing to the development of definite muscles which render an independent movement of the organ possible, as well as of glands. The tongue, moreover, is relatively larger, and the numerous papillæ render the surface velvet-like. Its mobility varies greatly in the different forms. It is usually attached only by the anterior end or by a portion of its ventral surface (Fig. 202): in other cases it is free all round, and in Spelerpes (Fig. 203) is capable of being extended far out of the mouth by means of a complicated mechanism, similar to that which occurs in the Chameleon amongst Reptiles.
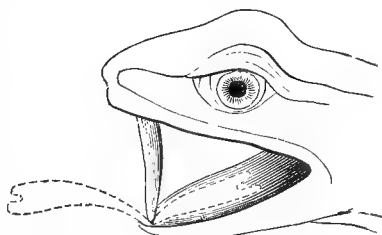
FIG. 202.—FIGURE SHOWING THE TONGUE OF THE FROG IN THREE DIFFERENT POSITIONS.

FIG. 203.—HEAD OF *Spelerpes fuscus*, WITH THE TONGUE EXTENDED.

**Reptiles.**—In most Reptiles the tongue is usually freely moveable, but its form and relative size varies greatly [1] (Fig. 204, A to E). It is provided with numerous sensory organs, but no glands are present in the tongue itself. It is least mobile in Chelonians and Crocodiles: in Snakes and many Lizards it is forked at the apex, and in the Chameleon it is protrusible, as in Spelerpes.

**Birds.**—The tongue of Birds is usually poorly provided with muscles. It possesses a horny covering, usually provided with papillæ and pointed, recurved processes; it may, as in many

[1] Thus in Lizards the tongue is used for classificatory purposes (*Vermilinguia, Crassilinguia, Brevilinguia, Fissilinguia*).
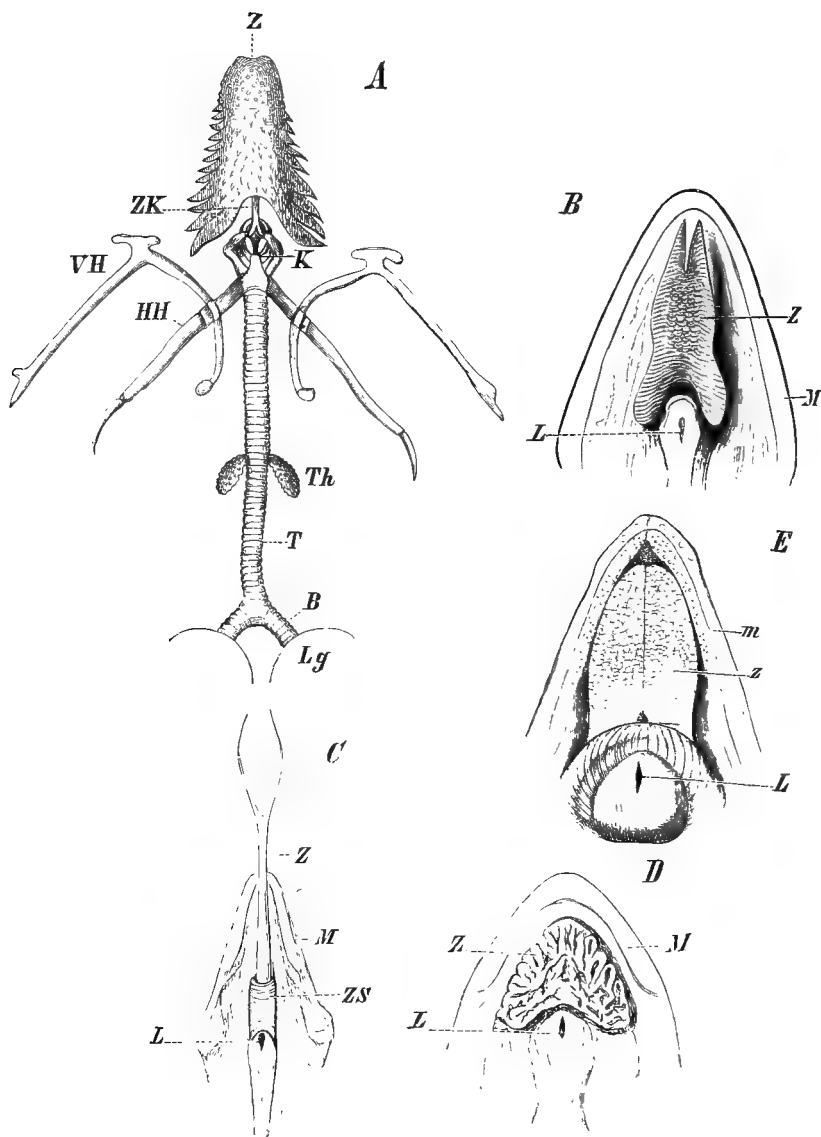
FIG. 204. -A, TONGUE, HYOID APPARATUS, AND BRONCHI OF A GECKO (*Phylodactylus europæus*) : B, TONGUE OF *Lacerta* ; C, OF *Monitor indicus*; D, OF *Emys europæa* ; E, OF AN ALLIGATOR.

*Z*, tongue ; *ZK*, body of hyoid ; *VH* and *HH*, anterior and posterior cornua of hyoid ; *K*, larynx ; *Th*, thyroid ; *T*, trachea ; *B*, bronchi ; *Lg*, lung ; *M*, mandible ; *L*, glottis ; *ZS*, sheath of tongue.

Reptiles, be split up at its distal end, being either bifurcated (Trochilidæ) or having a brush-like form. In Woodpeckers (the extraordinarily developed epibranchials of which have already been mentioned in the chapter on the skull), the tongue may be thrown far out from the mouth by means of a complicated system of muscles, and it thus serves as a prehensile organ.

The tongue is largest in predatory Birds (Rapaces) and Parrots, but its size is here not due so much to the special development of muscles as to the presence of fat, vessels, and glands.

**Mammals.**—The tongue reaches its most complete morphological and physiological development in Mammals, and, as elsewhere, undergoes the most various modifications in form. It is as a rule flat, band-like, rounded anteriorly, and extensile. Intrinsic as well as extrinsic muscles are well developed. A fold, the so-called *sublingua* (plica fimbriata), is present on the lower surface of the tongue, and is especially well marked in Lemurs; in the Slender Loris (Stenops) it is supported by cartilage. This probably corresponds to the last vestige of the tongue of lower Vertebrates which has been replaced by the more highly-developed organ characteristic of Mammals. The latter has probably arisen from the posterior part of the degenerated sublingua.

## THYROID.

The thyroid arises primarily as a median ventral diverticulum of the pharynx in the region of the first four or five visceral clefts, and in the course of development may become subdivided into two lobes. In addition to this unpaired diverticulum, paired portions, situated more posteriorly, are developed in Mammals.

. In the Ammocœte the single diverticulum, which is lined by a ciliated epithelium, opens into the pharynx between the third and fourth clefts (Fig. 221), but in the adult Petromyzon the organ, as in all Vertebrates, loses its connection with the pharynx, undergoes a modification, and gives rise to numerous closed glandular vesicles enclosing an albuminous substance.

In Elasmobranchs the thyroid is unpaired and lies beneath the mandibular symphysis; in adult Teleosts it is paired, and is situated in the region of the first branchial arch. In Dipnoans it lies anteriorly to the muscles of the visceral skeleton and shows an indication of a division into right and left lobes.

In the Urodela and Anura the thyroid gives rise to numerous vesicles situated close to the anterior end of the pericardium, posteriorly to the second ceratobranchials in the former and on the ventral side of the posterior cornua of the hyoid in the latter.

In Lizards it is usually situated close to the trachea (Fig. 204, A), and in Chelonians and Crocodiles it often possesses right

and left lobes lying on the great vessels just after they leave the heart. In Birds (Fig. 205) the organ is paired, and lies close to the origin of the carotid arteries.

The thyroid of Mammals consists of two lobes often connected by a median isthmus, situated on the ventral side of the larynx and trachea (Fig. 190).

It appears probable that the thyroid represents a very ancient glandular organ, the secretory function of which in relation to the alimentary canal was of great importance in the ancestors of Vertebrates. In existing forms it has undergone a change of function, and thus instead of disappearing, remains as an important organ in the adult: in Mammals especially it is characterised by a great richness in bloodvessels. What this function is, is not thoroughly understood, but it has been shown that its albuminous secretion contains iodine, and is passed into the blood- and lymphvessels; and that extirpation of the organ is followed by various disturbances of the mental and organic functions.

The structure known as the "carotid gland" in Mammals, which is situated at the bifurcation of the common carotid into external and internal carotids, has not, as was formerly supposed, anything to do with the thyroid or thymus. It is abundantly provided with nerve-cells.

THYMUS.

The thymus has always a paired origin, and in the adult consists of lymphoid tissue. In Elasmobranchs it arises on either side from the epithelium lining the upper part of the first five gill-clefts, close to the ganglia of the ninth and tenth cerebral nerves, as well as in the neighbourhood of the spiracle. The function of this organ, though doubtless a very important one, is not understood.
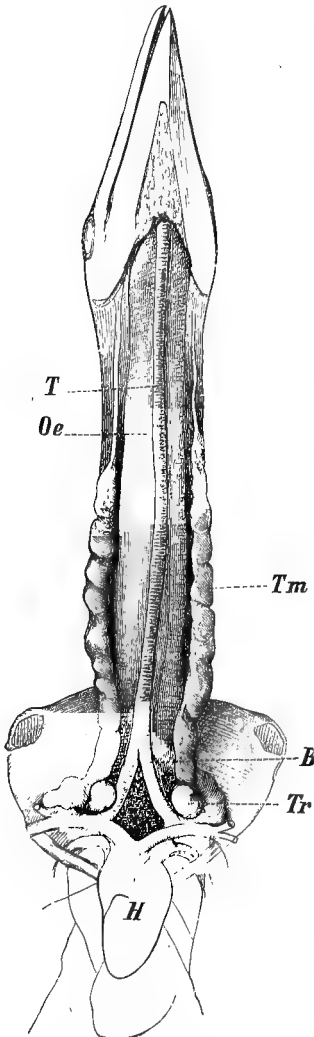


FIG. 205.—THYMUS AND THYROID OF A YOUNG STORK.

*T*, trachea; *B*, bronchi; *Oe*, œsophagus; *H*, heart; *Tm*, thymus; *Tr*, thyroid.

In Fishes and Dipnoans the thymus is more or less subdivided, and is situated dorsally to the gill-arches. In Amphibians it lies behind and above the articulation of the lower jaw, and in Reptiles in the neighbourhood of the carotid artery, either close in front of the heart (*e.g.*, Snakes) or more anteriorly. In Birds, as in young Crocodiles, it is elongated and more or less lobed, extending all along the neck (Fig. 205). In Mammals the greater part of the thymus is situated in the thorax, between the sternum and heart, only a small portion extending into the neck. It is largest in young animals, and usually becomes more or less completely degenerated subsequently.

### ŒSOPHAGUS, STOMACH, AND INTESTINE.

**Ichthyopsida.**—The œsophagus is short, and usually not distinctly marked off from the stomach, though exceptions to this rule often occur (*e.g.*, many Teleostei, Siren lacertina Fig. 210, A).

The stomach is often defined as a widened section of the enteric canal situated between the posterior end of the gullet and the entrance of the bile duct. Such a dilatation cannot accurately be spoken of as a stomach unless its epithelium possesses specific characteristics and gives rise to *gastric glands* (p. 267); in this sense a stomach is wanting in Amphioxus, Cyclostomi, Holocephali, certain Teleostei (*e.g.*, Cyprinidæ, certain Labridæ, Gobiidæ, Bleniidæ, Syngnathus acus, Cobitis fossilis), and Dipnoi (Fig. 209). Whether this is a primitive character in these forms or is due to degeneration is uncertain.

In other Fishes (Elasmobranchs, Ganoids, numerous Teleosts), as well as in all Amphibians, a true stomach is present, and is usually externally recognisable as a more or less dilated sac; it may be curved on itself, so as to form a U-shaped loop, the two (cardiac and pyloric) limbs of which lie parallel to one another (Fig. 206). In general, its form is adapted to that of the body: thus Rays and Anurans possess a far wider stomach than do most other Fishes and Amphibians (comp. Figs. 206—210), and this rule holds good also for Reptiles. The stomach of Teleosts varies considerably in form.[1]

The intestine may be straight or nearly straight, or may be more or less coiled, and in the former case a *spiral fold* or *valve* may be developed in Fishes, to increase the absorptive surface.

In the Lamprey a longitudinal fold or *typhlosole*, taking a slightly spiral course, extends into the lumen of the intestine. In Elasmo-

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[1] In numerous Teleosts (*e.g.*, Tinca vulgaris, Cobitis fossilis) outer longitudinal and inner circular *striated* fibres are present in both stomach and intestine externally to the unstriated muscular coat. They grow backwards from the œsophagus.

S
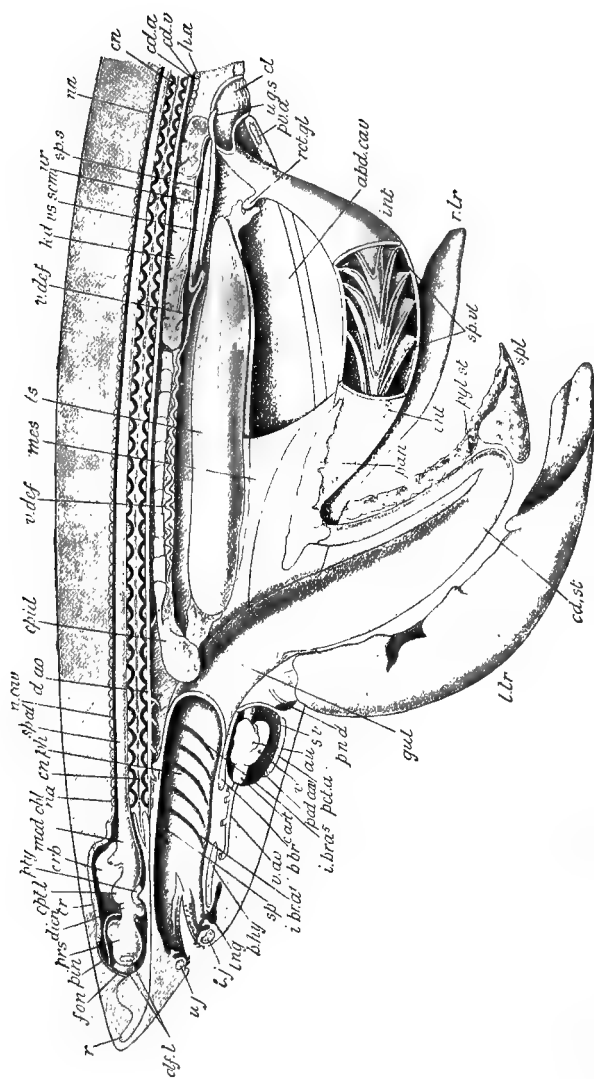
FIG. 206.—DISSECTION OF A MALE *Scyllium canicula*, from the left side. (From T. J. Parker's *Elementary Biology*). The left side of the body wall is cut away to the median plane so as to expose the abdominal (*abd. cav.*), pericardial (*prd. cav.*), and neural (*n. cav*) cavities in their whole length.

In the skeleton the cartilaginous parts are dotted, the bony ends of the centra (*cn*) black. *n.a*, neural arches; *h.a*, hæmal arches; *cr*, cranium; *r*, rostrum; *u.j*, upper jaw; *l.j*, lower jaw; *b.hy*, basi-hyal supporting tongue (*tng*); *b.br*, basi-branchial; *pct.a*, pectoral arch; *pv.a*, pelvic arch; *fon*, fontanelle. The alimentary canal with the liver (*l.lr*, *r.lr*), &c., has been displaced downwards, and the oral cavity and pharynx (*ph*), part of the intestine (*int*), and the cloaca (*cl*) have been opened. *sp*, spiracle; *i.br.a¹—i.br.a⁵*, internal branchial apertures; *œl.st*, cardiac, and *py.st*, pyloric portions of stomach; *sp.vl*, spiral valve of intestine (*int*); *pan*, pancreas; *spl*, spleen; *rct.gl*, rectal gland; *mes*, mesentery. *s.v*, sinus venosus; *au*, auricle; *v*, ventricle; *c.art*, truncus arteriosus; *v.ao*, ventral aorta with origins of the afferent branchial arteries; *d.ao*, dorsal aorta, receiving the efferent branchial arteries anteriorly, and posteriorly becoming the caudal artery (*cd.a*) lying above the caudal vein (*cd.v*).

*sp.c*, spinal cord; *med.obl*, medulla oblongata; *crb*, cerebellum; *opt.l*, optic lobes; *dien*, thalamencephalon; *prs*, prosencephalon; *olf.l*, olfactory lobes; *pin*, pineal body; *pty*, pituitary body. *kd*, left kidney; *ur*, duct of kidney; *u.g.s*, urinogenital sinus; *ts*, left testis; *epid*, epididymus; *v.def*, vas deferens; *vs.sem*, vesicula seminalis; *sp.s*, sperm-sac; *p.n.d*, rudimentary Müllerian duct.

branchs, Ganoids, and Dipnoans, the fold is more highly developed
and forms a well-marked spiral valve, the
turns of which may lie so close together
as to almost fill the cavity of the intestine
(Figs. 206, 207, 209). In the Ganoids it
begins to undergo degeneration; thus in
Lepidosteus (Fig. 207) it is only present
in the hinder part of the intestine.
Traces of a spiral valve can even be re-
cognised amongst the Teleostei (Cheiro-
centrus and possibly certain Salmonidæ).

*Pyloric cæca* are met with in Ganoids
and numerous Teleosts, and consist of
longer or shorter finger-shaped processes
of the small intestine, situated posteriorly
to the pylorus in the region of the bile-
duct (Figs. 207 and 208). Their number
varies from 1 (Polypterus and Ammo-
dytes) to 191 (Scomber scomber). The
pyloric cæca and spiral valve seem to have
a similar function, and, as a general rule,
to be developed in inverse proportion to
one another.

In the narrow-bodied Gymnophiona
the intestine is only slightly coiled, while
in Anura it becomes considerably folded
on itself: its form in Salamanders is about
mid-way between these two extremes.

In the Cyclostomi, Holocephali,
Ganoidei, and most Teleostei, there is
a separate anus; in all other Fishes as
well as in the Dipnoi and Amphibia the
large intestine opens into a *cloaca* common
to it and to the urinogenital ducts. The
large intestine (rectum) is comparatively
short and takes a straight course; in
Amphibians, as well as to some extent
in certain Ganoids and Teleosts, it is
plainly marked off from the small
intestine, and between the two there is
often a circular valve. In some cases
the rectum is considerably swollen and
may even exceed the stomach in cap-
acity (Fig. 210, *B*). An outgrowth of
the ventral wall of the cloaca in Am-
phibia gives rise to the *urinary bladder*,
and represents the *allantois* (p. 9) of
higher forms.
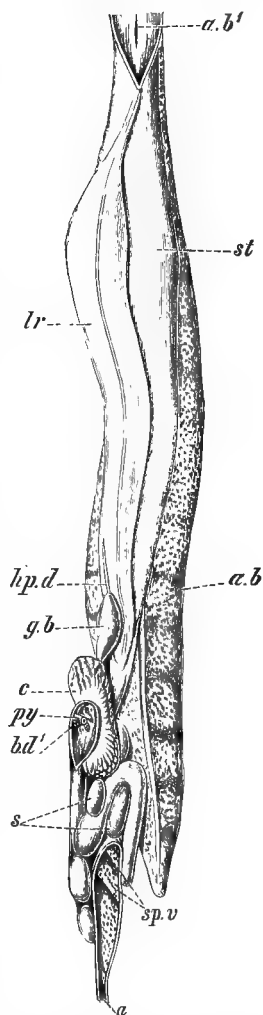


FIG. 207.—ALIMENTARY VIS-
CERA AND AIR-BLADDER OF
*Lepidosteus, in situ.* (After
Balfour and Parker.)

*a*, anus; *a.b*, air-bladder;
*a.b'*, its aperture into the
throat; *b.d¹*, aperture of
bile-duct into intestine; *c*,
pyloric cæca; *g.b*, gall-
bladder; *hp.d*, hepatic
duct; *lr*, liver; *py*, pyloric
valve; *s*, spleen; *sp.v*, spiral
valve; *st*, stomach.
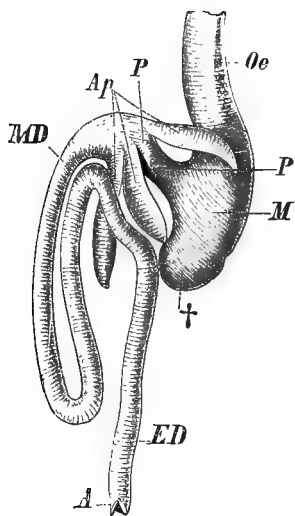
FIG. 208.                                    FIG. 209.

FIG. 208.—ALIMENTARY CANAL OF PERCH.

*Oe*, œsophagus ; *M*, stomach ; †, cæcal process of latter ; *P—P*, short pyloric
region ; *Ap*, pyloric cæca ; *MD*, small intestine ; *ED*, rectum ; *A*, anus.
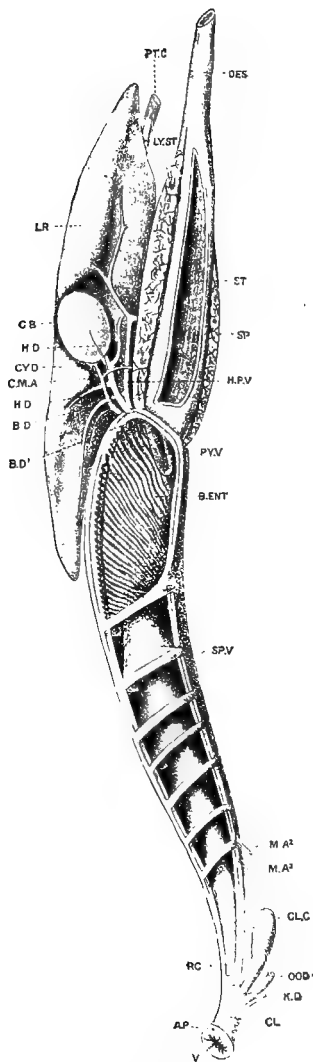
FIG. 209.—ALIMENTARY CANAL AND APPENDAGES OF *Protopterus annectens*.
(After W. N. Parker.)

*o s*, œsophagus ; *st*, "stomach" ; *py.v*, pyloric valve ; *b.ent*, bursa entiana
(anterior portion of intestine) ; *sp.v*, spiral valve ; *rc*, rectum ; *cl*, cloaca ;
*cl.c*, cloacal cæcum ; *v*, vent ; *a.p*, abdominal pore ; *ood*, base of oviduct ;
*k.d*, base of kidney duct ; *lr*, liver ; *g.b*, gall-bladder ; *h.d*, hepatic ducts ;
*cy.d*, cystic duct ; *b.d*, common bile duct, and *b.d¹*, its aperture into the
intestine ; *c.m.a*, cœliaco-mesenteric artery ; *m.a²*, *m.a³*, mesenteric arteries ;
*h.p.v*, hepatic portal vein ; *sp*, spleen. The pancreas is not seen, as it is
embedded in the walls of the "stomach" and anterior part of the intestine
on the dorsal and right side.
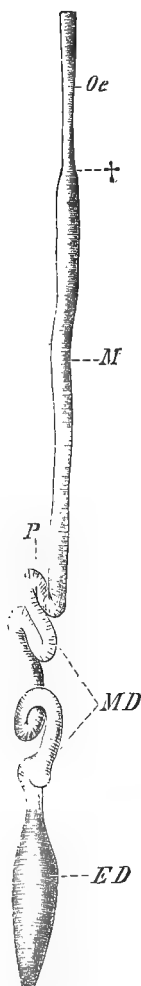
FIG. 210A.                        FIG. 210B.

FIG. 210A.—ALIMENTARY CANAL OF *Siren lacertina.*

*Oe,* œsophagus, marked off from the stomach (*M*) by a constriction, †; *P*, pyloric region; *MD,* small intestine; *ED,* large intestine.
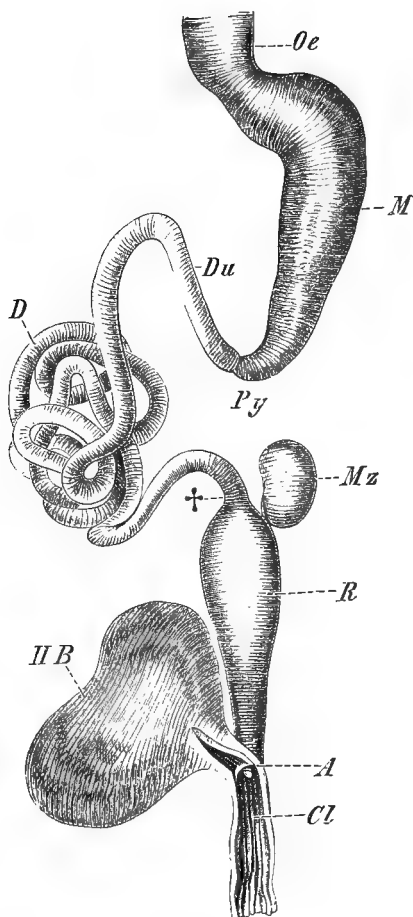
FIG. 210B.—ALIMENTARY CANAL OF *Rana esculenta.*

*Oe,* œsophagus; *M,* stomach; *Py,* pyloric region; *Du,* duodenum; *D,* ileum; †, boundary between the latter and the large intestine (*R*); *A,* opening of the rectum into the cloaca (*Cl*); *Hb,* urinary bladder; *Mz,* spleen.

In Elasmobranchs a finger-shaped *rectal gland* (*processus digitiformis*) opens into the anterior part of the rectum, and this perhaps corresponds to the cæcum of higher forms (see pp. 262, 266). Traces

of a cæcum are seen in certain Teleosts. In the Dipnoi a cloacal cæcum is present (Fig. 209).

In all Fishes in which a cloaca is absent (p. 259) the anus is anterior to the urinogenital aperture.


**Reptiles.**—In correspondence with the more definitely differentiated neck, the œsophagus of Reptiles is relatively longer than in the animals as yet considered; it is always plainly marked off from the much wider stomach, which is usually sac-like, or bent upon itself, in which latter case it lies transversely (Chelonians).[1] As regards external form, the stomach of Crocodiles is more specialised than that of other Reptiles, approaching that of Birds.

Snakes, Snake-like Lizards, and Amphisbænians possess a narrow, spindle-shaped stomach, which lies in the long axis of the body; in correspondence with the large size of the masses of food, which are swallowed whole, it is capable of great distension. In these the intestine is only slightly coiled: in Lizards the coils are more marked, and in the other forms, with broad bodies, the folding is carried still further.

The large intestine has a straight course, is often considerably swollen, and opens into a cloaca. It may (*e.g.*, certain Chelonians) be as long as the small intestine and be bent on itself. An account of the urinary (allantoic) bladder present in many Reptiles will be found in a subsequent chapter.

From the Reptilia onwards a blind-gut or *cœcum* is usually formed at the anterior portion of the large intestine: it is generally asymmetrical.


**Birds.**—In correspondence with the kind of nutriment, the mode of life, and the absence of teeth, certain modifications of the œsophagus and stomach occur in Birds. In graminivorous Birds and Birds of Prey either the whole gullet forms a dilated sac or else it gives rise to a ventral outgrowth; in both cases the enlargement is known as the *crop* (*ingluvies*) (Fig. 211). This serves as a food reservoir, and in some cases its walls are glandular.

The stomach, instead of remaining simple, generally becomes divided externally into two portions, an anterior and a posterior (Fig. 211). The former, which on account of its richness in glands is called the glandular stomach (*proventriculus*), alone takes part in dissolving the food; while the latter, which is lined by a horny layer consisting of a hardened glandular secretion, has simply a mechanical function, in correlation with which a peculiar and very thick muscular wall provided with two tedinous discs is developed. The degree of development of this muscular stomach, or *gizzard*, stands in direct proportion to the consistency of the food. In

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[1] The œsophagus of marine Chelonians, like that of many Birds, is lined by horny papillæ.

graminivorous Birds we find the strongest muscular layer and the thickest horny lining, while in the series of insectivorous Birds, up to the Birds of Prey, this condition becomes gradually less marked, and the division of labour is less noticeable.

Thus in the series of existing Birds we can trace the course of the phylogenetic differentiation of the organ.

The small intestine is usually of considerable length and becomes folded on itself to a greater or less degree; it varies, however, both in form, length, and diameter.

The straight large intestine opens into a cloaca, and varies as to its relative diameter. The cæcum is usually paired, and may reach a relatively enormous length (Lamellirostres, Rasores, Ratitæ). All kinds of intermediate stages between this and an entire absence of a cæcum are to be met with. When the cæcum is largely developed, it has an important relation to digestion, as an increase of surface of the mucous membrane is thus effected; this increase may even be carried further by each cæcum being provided with a spiral fold consisting of numerous turns, as in the Ostrich.

The so-called *bursa Fabricii* is a structure peculiar to Birds, and arises as a small, solid, epithelial outgrowth from the ectodermal portion of the cloaca, later becoming excavated to form a vesicle. It is situated in the pelvic cavity between the vertebral



Fig. 211.—Diagram of the Œsophagus and Stomach of a Bird.

*Oe, Oe¹*, œsophagus; *Ig*, crop; *DM*, glandular stomach; *MM*, muscular stomach; *MD*, duodenum.

column and the posterior portion of the intestine, and extends to the outer section of the cloaca, into which it opens posteriorly to the urinogenital ducts. It is probably present in all Birds, but becomes atrophied more or less completely in the adult; its physiological function is quite unknown.

**Mammals.**—The œsophagus, like that of Birds, is sharply marked off from the stomach, and its muscles consist to a greater or less extent of striated fibres: in Ruminants the latter extend as far as the stomach.

The stomach undergoes much more numerous modifications than are met with in any other Vertebrate Class. As a rule it takes a more or less transverse position and has a sac-like form, the cardiac portion, into which the œsophagus opens, being usually more swollen and having thinner walls than the pyloric portion which communicates with the duodenum.

According to the definition given on p. 257, a true stomach is

FIG. 212.—DIAGRAMS OF THE STOMACH IN VARIOUS MAMMALS SHOWING THE DIFFERENT REGIONS. (After Oppel.)

A, ORNITHORHYNCHUS ANATINUS; B, KANGAROO (*Dorcopsis luctuosa*); C, TOOTHED WHALE (*Ziphius*); D, PORPOISE; E, HORSE; F, PIG; G, HARE; H, HAMSTER (*Cricetus frumentarius*).

(The œsophageal region (lined by stratified epithelium) is indicated by transverse lines; the region of the cardiac glands by oblique lines; that of the fundus glands by dots, and that of the pyloric glands by crosses.)

*Oes*, œsophagus; *P*, pylorus; *D*, duodenum; *I—IV* (in D), the four chambers of the stomach; *l* (in B), lymphoid tissue; *x...x* (in B), boundary line between the œsophageal and cardiac regions; *f* (in H), fold bounding the œsophageal region.

wanting in Monotremes (Fig. 212, A): although the organ is represented by a wide sac, it is entirely wanting in glands, and is lined throughout by a stratified epithelium. This remarkable condition is doubtless due to degeneration. Amongst Edentates, a similar peculiarity is seen in Manis javanica—in which, however, the glands are retained in a sac-like outgrowth from the greater curvature, and in Sloths—in which the glands are more numerous.

In herbivorous Mammals the stomach is, as a rule, relatively larger and more complicated than in carnivorous Mammals
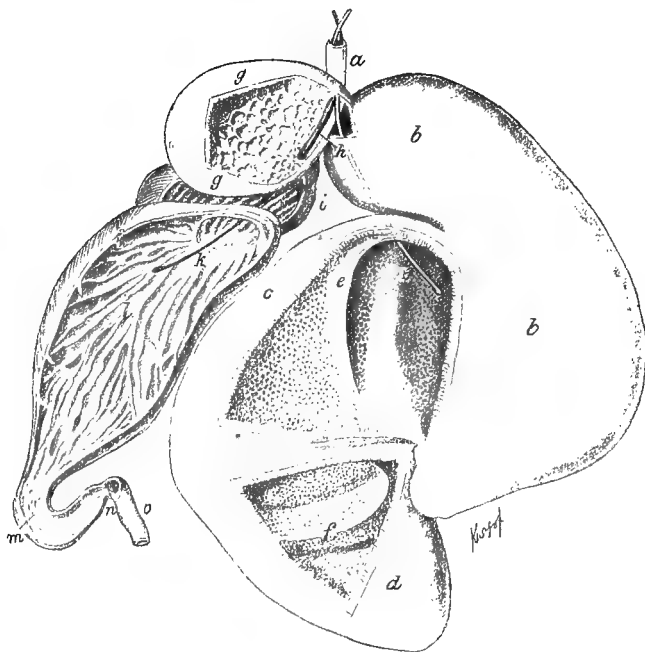


FIG. 213.—STOMACH OF SHEEP.    (From Oppel.    After Carus and Otto.)

a, œsophagus ; b. c, d, the three subdivisions of the paunch, marked off from one another by the folds e and f; g, reticulum ; h, œsophageal groove ; i, psalterium ; k, aperture leading from the psalterium into the abomasum (l, m) ; n, pyloric valve ; o, duodenum.

(Figs. 212 and 213), and it may become divided into two or more chambers. In some Rodents and in the Horse distinct cardiac and pyloric chambers can be recognised, and in Ungulates numerous intermediate forms between a simple and an exceedingly complex stomach, such as occurs in the typical Ruminants, are to be met with. In the latter (Fig. 213) the stomach is divided into four chambers, which are called respectively *rumen (paunch), reticulum, psalterium,* and *abomasum.* The two first, which may be looked

upon as parts of one and the same chamber, simply serve as storage cavities, the food returning from them into the mouth, once more to undergo mastication. It then passes into the psalterium, and finally into the abomasum, the latter alone being provided with gastric (rennet) glands, and serving as the true digestive stomach. The psalterium is the latest to be differentiated both phylo- and ontogenetically, and is rudimentary in the Tragulidæ. In Camels the rumen gives rise to two masses of gland-containing outgrowths, known as "water-cells." In the Cetacea (Fig. 212, C and D), Hippopotamus, and Bradypus, the stomach is divided into several chambers, and various other modifications in form and structure are met with amongst Mammals. Thus in the Kangaroo, for instance (Fig. 212, B), the walls of the stomach are curiously folded.

The small intestine is usually long, and varies more as to relative length and diameter in domesticated than in wild forms.

The large intestine, which is made up of a varying number of coils, usually reaches a great length, and its diameter is much greater than that of the small intestine : these two portions are thus sharply marked off from one another, and the distinction between them is rendered still more marked by the sacculations of the anterior part of the large intestine. Only the posterior portion of the latter, or *rectum*, which passes into the pelvic cavity, corresponds to the large intestine of lower Vertebrates ; the remaining and far larger part occurs only in Mammals, and is called the *colon*.

The cæcum, which is almost always present, undergoes various modifications both as to form and size. Thus in Edentates (Manis, Bradypus), Carnivora, Odontoceti, Insectivora, and Cheiroptera, it is very small or even entirely wanting, while in Herbivora it may exceed the whole body in length. An inverse development in size is usually noticeable between it and the rest of the large intestine. In many cases (many Rodents, Monkeys, and Man) an arrest of a portion of the cæcum takes place in the course of individual development, so that little more than the distal end (*processus vermiformis*) remains (Fig. 190). In Lepus the enormous cæcum is provided with a spiral valve ; and in Hyrax, besides a large sacculated cæcum at the junction of the small and large intestines, there is a pair of large, simple, conical cæca further back.

Monotremes only amongst Mammals possess a distinct cloaca, though in Marsupials and some Rodents the anal and urinogenital apertures are surrounded by a common sphincter. In other Mammals these apertures become completely separated from one another.

HISTOLOGY OF THE MUCOUS MEMBRANE OF THE ALIMENTARY
CANAL.

The epithelium lining the alimentary canal of Vertebrates—with
the exception of that of the mouth and cloaca, which is usually
stratified—consists primitively, that is, phylogenetically, of amœboid
or cilated cells.   In some cases this is also true ontogenetically, and
in Amphioxus and Protopterus, for instance, the ciliated epithelium
persists throughout life, and in the Ammocœte until metamorphosis.
In the adult Petromyzon, as well as in many Fishes and even Amphi-
bians, ciliated epithelium occurs constantly only in certain parts of
the gut, and in the higher Vertebrates cilia are only seen excep-
tionally after the embryonic period, so that, as a rule, only ordinary
columnar epithelium is present.   A striated margin is observable
along the free border of the columnar cells (Fig. 214, A, B, a) ; this
is probably to be looked upon as the expression of the earlier
ciliated covering, and in some lower Vertebrates (e.g., Proteus and
Salamander larvæ) it is capable of an active amœboid movement
(B, b).   In this active participation of the cells in the process of
absorption, we recognise an old inheritance from primitive Inver-
tebrates (intracellular digestion) ; but, at the same time, extra-
cellular or chemical digestion is the more important and occurs
exclusively in the higher types.

Numerous lymph-cells or leucocytes (p. 299) are present in great
numbers in the connective-tissue layer of the mucous membrane,
and often form definite masses or follicles (e.g., " Peyer's patches ").
In some cases (e.g., Protopterus), the development of this lymphatic
tissue along the gut is relatively enormous (comp. p. 334).   The
amœboid leucocytes may even force their way into the lumen of
the intestine : a similar migration of these cells occurs in all
mucous membranes and in the walls of many vessels.

In Amphioxus, Cyclostomi, and Dipnoi, the whole of the
alimentary epithelium must be considered as secretory, each
individual cell acting as an independent gland.   In Fishes,
Amphibians, and Reptiles, a higher stage is reached, inasmuch
as groups of cells in the stomach gives rise to tubular glands of a
simple nature (Fig. 214).[1]   A further differentiation of the cells
leads to the condition seen in the gastric glands of Mammals, in
which the cells become differentiated into chief cells and parietal cells.

According to their position, three kinds of glands can be dis-
tinguished in the stomach of Mammals, viz., cardiac, fundus-, and
pyloric glands.   The fundus glands have the greatest physiological
importance (comp. Fig. 212).

In the higher Vertebrates, more especially in Birds and
Mammals, the epithelium of the intestine also gives rise to tubular

[1] Even in Ganoids and Teleosts the cells of the neck and fundus of each gland
are said to be different in character, pepsin being formed in the latter.

structures known as the *crypts* or *glands of Lieberkühn*, as well as to acinous mucous glands.    Mucous-secreting goblet cells are
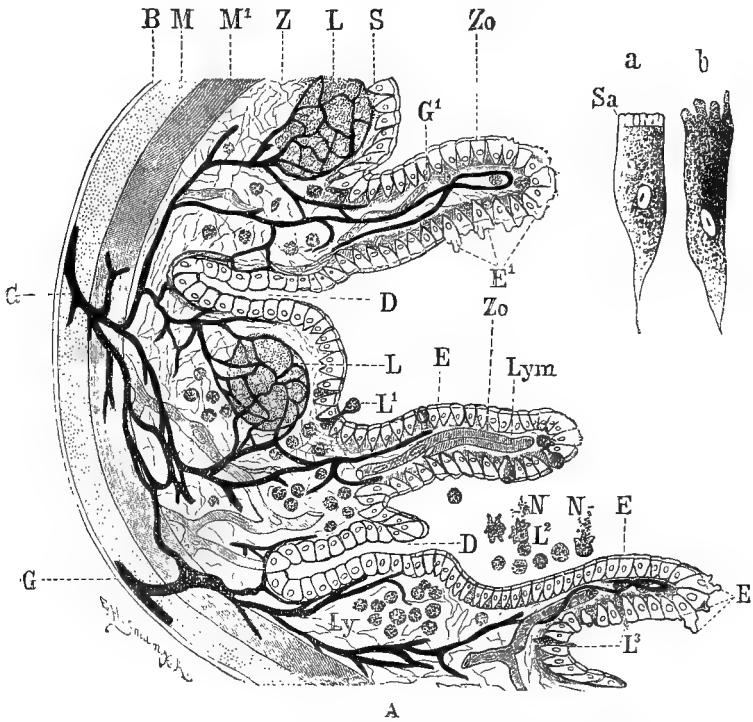


FIG. 214.—A, SEMIDIAGRAMMATIC TRANSVERSE SECTION OF A PORTION OF THE WALL OF THE INTESTINE.    (Combined from the condition seen in both lower and higher Vertebrates.)    B, Epithelial cells of the intestine.

*P*, peritoneal investment of the gut ; *M*, longitudinal muscular layer ; $M^1$, circular muscular layer ; *Z*, connective-tissue layer ; *S*, mucous membrane, which is raised to form villi at *Zo*.    (The connective-tissue layer and epithelium are designedly drawn much too large relatively as compared with the outer coats.)    *G, G*, vessels, the larger trunks running between the peritoneum and the muscular layer ; the finer vessels branch out into the intermediate layer ; these surround the masses of lymph-cells, *LL*, as well as the glands, and send fine loops into the villi (at $G^1$); *DD*, apertures of the glands ; *E, E*, epithelial cells of the mucous membrane, with their striated border, from which at $E^1$ amœboid processes are extruded : in Fig. B, *a, b*, these cells are drawn to a much larger scale (*Sa*, striated border) ; *Ly*, scattered lymph-cells in the intermediate layer ; $L^1, L^3$, lymph-cells in the act of passing through the mucous membrane ; at $L^2$, several have already passed into the alimentary cavity ; *LL*, masses of lymph-cells (solitary follicles) ; *Lym*, lymph-vessels in the villi.

common throughout the alimentary epithelium of Vertebrates. In Monotremes, as already mentioned (p. 265), gastric glands are absent, but the intestinal glands are highly developed.

In order to effect an increase of the absorptive surface, longitudinal folds of the mucous membrane are formed, and a special development of such a fold, taking a spiral course, may result in the formation of a spiral valve (see p. 257). A further advance is seen in the development of transverse folds between the longitudinal ones—these are already seen in Elasmobranchs and many other Fishes; and by still further modifications, crypts of varied
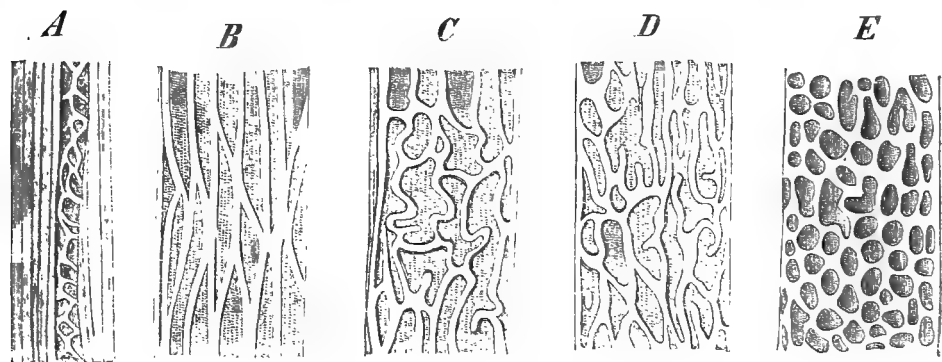


Fig. 215.—Semidiagrammatic Figures of the Mucous Membrane of the Intestine of Fishes, showing Intermediate Forms between Longitudinal Folds and Round Crypts.

*A*, Petromyzon, showing the distinct spiral fold; *B*, an Elsmobranch *C* to *E*, various Teleosts.

form and depth are produced, into which open the microscopic glands, when present (comp. Fig. 215).

Finger-shaped outgrowths or *villi* of the mucous membrane of the intestine are first plainly distinguishable in Amphibians (especially Anura) and are especially well developed in Mammals. In addition to these, folds of varied forms, on the surface of which the villi may be situated, occur from the Amphibia onwards : as examples may be mentioned the valvuli conniventes of Mammals and Birds.

## LIVER.

The liver, the form of which is always closely adapted to that of the surrounding parts, underlies to a greater or less extent the ventral side of the intestinal tract, and is present in all the Craniata. It arises as an outgrowth from the endodermic epithelium of the intestine close to the junction of the latter with the stomach.

In Amphioxus a simple sac-like cæcum is present in this
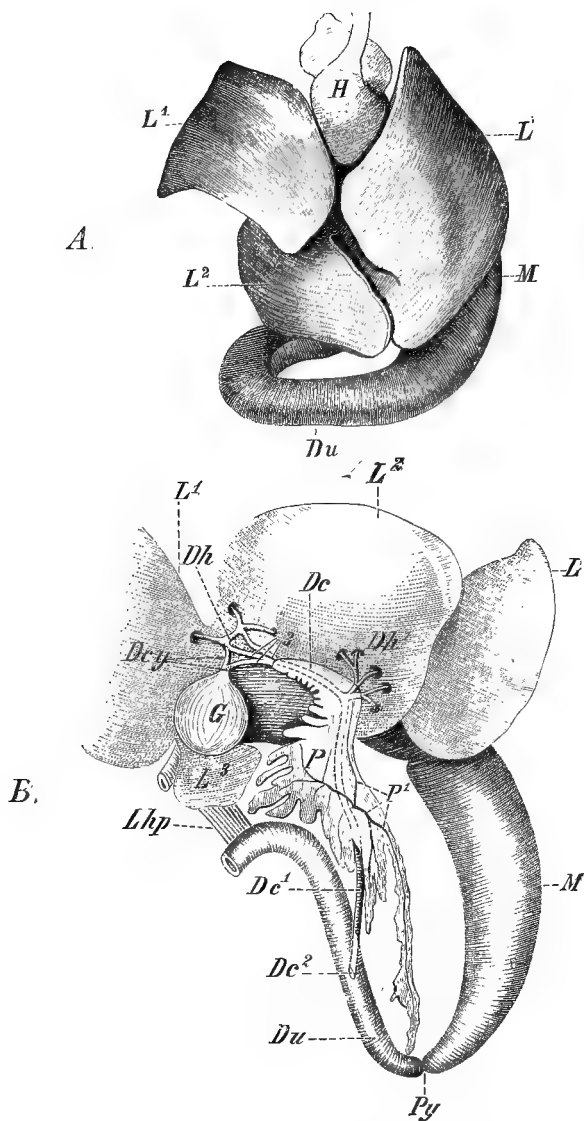
FIG. 216A.—LIVER OF *Rana esculenta*. (From the ventral side.)
L, $L^1$, $L^2$, the different obes of the liver ; M, stomach ; Du, duodenum ;
H, heart.

FIG. 216B.—PANCREAS AND LIVER OF FROG, TO SHOW THE ARRANGEMENT OF
THEIR DUCTS.

L, $L^1$, $L^3$, the lobes of the liver turned forwards ; G, gall-bladder ; Dcy, cystic
ducts, which, together with the hepatic ducts (Dh), form a network from
which three collecting ducts arise, and these unite to form the common bile-
duct (Dc): the latter passes through the substance of the pancreas (P),
receiving further hepatic ducts ($Dh^1$), and the pancreatic ducts ($P^1$); at
$Dc^1$ it becomes free from the pancreas, and passes back to open into the
duodenum (Du) at $Dc^2$ ; Lhp, duodeno-hepatic omentum ; M, stomach ; Py,
pylorus.

region which possibly represents the rudiment of the liver (Fig. 219). In Craniates the outgrowth develops into a large vascular and glandular organ, which gives rise to bile, and remains in communication with the intestine by means of one or more *bile-ducts* [1]
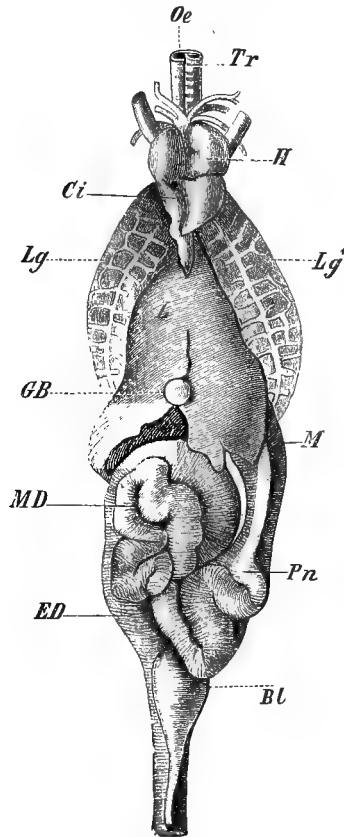


FIG. 217.—VISCERA OF *Lacerta agilis.* (From the ventral side.)

*Oe,* œsophagus ; *M,* stomach ; *MD,* small intestine ; *ED,* large intestine ; *L,* liver ; *GB,* gall-bladder ; *Pn,* pancreas ; *Bl,* urinary bladder ; *Lg, Lg¹,* the two lungs, with their network of vessels ; *H,* heart ; *Ci,* postcaval, *Tr,* trachea.

(Figs. 206, 209, and 216–218). It is united to the body-wall by a fold of the peritoneum, and varies considerably in the number of its lobes : in Mammals there may be as many as six or seven (*e.g.,* Dog, Weasel). We may nevertheless fix upon a ground-form consisting

[1] The single-lobed liver of the Lamprey undergoes a histological retrogression (fatty metamorphosis) after transformation. The tubuli disappear, the cells become filled with fat, and the gall-bladder and bile-duct become atrophied.

of two lobes as the primary one in all Vertebrates.   The liver of the Anamnia is usually relatively larger than that of the Amniota.

Carnivorous (fat-eating) animals generally possess a larger liver than Herbivores.

A *gall-bladder* is very commonly present partially imbedded in the right primary lobe.   It is connected with the system of *hepatic*
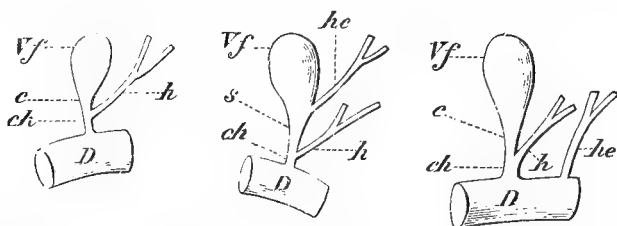


FIG. 218.—A, B, C, VARIOUS MODIFICATIONS IN THE ARRANGEMENT OF THE BILE-DUCTS.

*D*, duodenum ;  *Vf*, gall-bladder ;  *c* and *s*, cystic duct ;  *h*, hepatic duct ;  *ch*, common bile-duct ;  *hc*, hepato-cystic duct ;  *he*, hepato-enteric duct.

*ducts* by means of a *cystic duct*, thus forming a *common bile-duct* which opens into the anterior part of the intestine (duodenum). Some of the chief variations in the relative arrangement of these ducts are shown in Fig. 218.

## PANCREAS.

The pancreas arises from the proximal portion of the small in-testine, near the liver, in the form of several (usually two dorsal and one ventral) independent endodermic outgrowths : these may become fused later, or certain of them may undergo degeneration. Thus in the adult there may be a single duct, or several inde-pendent ducts opening into the intestine (*e.g.*, Birds, Crocodiles, Emydæ, and some Mammals) or in some cases into the bile-duct (Fig. 216, B).   Varying much in form and size, the pancreas early gives rise to a band-shaped or more or less lobulated organ, usually lying in the fold of the duodenum.   In some cases it remains em-bedded within the wall of the gut (*e.g.*, Protopterus,[1] Fig. 209), and amongst Teleosts (in which Order the pancreas was formerly sup-posed to be absent in the adult) it may be surrounded by the liver or have the form of scattered lobules extending throughout the mesentery.

[1] In Myxinoids a lobular gland is present in a similar relative position to the pancreas of Protopterus in the neighbourhood of the bile-duct, into which it opens : this probably corresponds to a pancreas.   A dorsal pancreas is also de-veloped in the embryo of Petromyzon, and a pancreas-like organ can be recognised in the adult.   The pancreas is not represented in Amphioxus.

## G.  ORGANS OF RESPIRATION.

THE respiratory organs of Vertebrates are closely connected with the alimentary canal both as regards position and development, and are of two kinds, **gills** and **lungs**.[1]  The former are phylogenetically the older organs, and are adapted for aquatic respiration : they are connected with the pharynx in the region of the visceral arches.  The latter always arise as sac-like outgrowths of the pharynx, which grow backwards so as to lie within the body-cavity.

Both gills and lungs may be developed in the same individual, but are usually not functional at the same time.  They are supplied with venous blood, which becomes purified while passing through their capillaries.

The *air-bladder* or *swim-bladder* present in many Fishes, and acting as a hydrostatic organ (p. 280), arises in a similar manner to the lungs—that is, as an outgrowth from the fore-part of the alimentary tract : it receives arterial blood from the aorta, and venous blood passes from it ; but in some cases (*e.g.*, Bony Ganoids and a few Teleosts) it may act as an accessory respiratory organ.


## I.  GILLS.

The gills arise in connection with a series of laterally-arranged outgrowths of the pharynx lying one behind the other, which become open to the exterior.  Passages or clefts are thus formed for the water entering by the mouth, and in order that oxygen may become absorbed, leaf-like or thread-like vascular processes, the *gills* or *branchiæ*, become developed in the region of each cleft.  These are *internal* or *external*, according to their position.[2]

Fishes possess gills throughout life ; amongst Amphibians this

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[1] The integument (*e.g.*, in Periophthalmus and Amphibia) and the intestine (*e.g.*, in Callichthys, Hypostomos, and Doras) may also take part in respiration.

[2] External gills persist after hatching as functional respiratory organs only in Polypterus, Calamoichthys, Protopterus, and the Amphibia, and in the Anura they are soon replaced by internal branchiæ (comp. pp. 278—280).
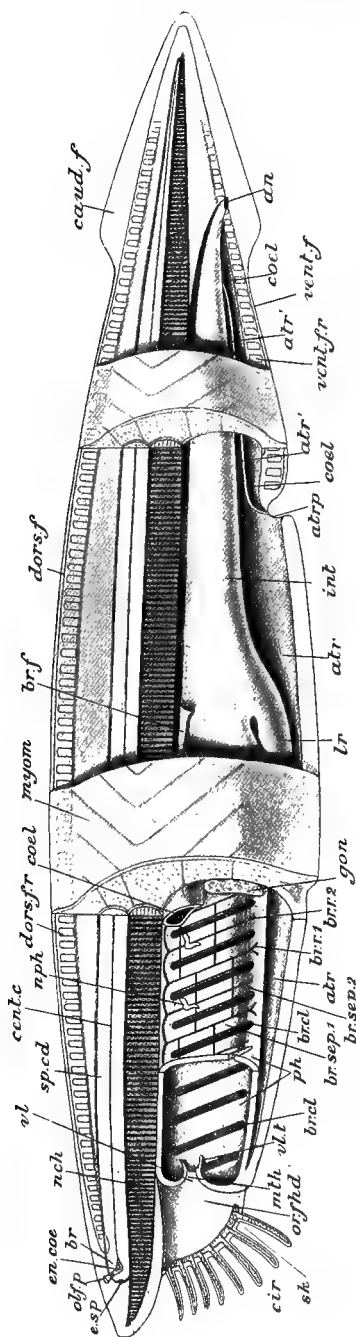
FIG. 219.—DIAGRAM OF THE ANATOMY OF AMPHIOXUS.  (From Parker and Haswell's *Zoology*.)

*an*, anus; *atr*, atrium; *atr′*, its posterior prolongation; *atrp*, atriopore; *br*, "brain"; *br.cl*, branchial clefts; *br.f*, brown funnel; *br.sep. 1*, primary, and *br.sep. 2*, secondary branchial lamella; *br.r. 1*, primary, and *br. r. 2*, secondary branchial rod; *caud.f*, caudal fin; *cent.c*, central canal; *cir*, cirri; *coel*, cœlome; *dors.f*, dorsal fin; *dors.f.r*, dorsal fin-rays; *en.coe*, ventricle of "brain"; *e.sp*, eye-spot; *gon*, gonad; *int*, intestine; *lr*, liver; *mth*, mouth; *myom*, myomeres; *nch*, notochord; *nph*, nephridia; *olf.p*, olfactory pit; *or.hd*, oral hood; *ph*, pharynx; *sk*, skeleton of oral hood and cirri (dotted); *sp.cd*, spinal cord; *vent.f*, ventral fin; *vent.f.r*, ventral fin-rays; *vel*, velum; *vlt*, velar tentacles.

is only the case in the Perennibranchiata : all the others simply pass through a gilled stage, and later breathe by means of lungs. Thus the study of this one Order furnishes us with an excellent representation of the course of phylogenetic development through which all the higher Vertebrates must have passed, and which is still indicated in them by the appearance in the embryo of gill-clefts and gill-arches with a corresponding arrangement of the blood-vessels. These occur throughout the entire series of the Amniota up to Man—that is, in forms in which they are no longer concerned in respiration.

Thus rudiments of five clefts are seen in the embryos of most Reptiles and Birds, and of four in Mammals ; in many cases, however, they do not become open to the exterior. Their order of disappearance is from behind forwards, and the most anterior (hyoid) cleft persists in a modified condition even in the adult, undergoing a change of function in connection with the auditory organ (p. 224). Certain of the anterior arches persist in a modified form (p. 69).

**Amphioxus.**—The numerous (80—100, or more) gill-clefts of Amphioxus, which are arranged in pairs and are supported by elastic rods, extend backwards nearly to the middle of the body. At first they open freely to the exterior, but at a later period of development they become enclosed in an *atrial* or *peribranchial chamber*, which opens by a single pore situated somewhat behind the middle of the body (for details compare Fig. 219).

The relative extent of the branchial apparatus is considerably limited even in the lowest Craniata.

**Cyclostomes.**—In the larval Ammocœte the œsophagus is continued directly backwards from the pharynx (Fig. 220, A), and at the anterior end of the latter there is a muscular fold, the *velum*, covered by the mucous membrane (Fig. 221).

The seven gill-sacs provided with leaf-like folds of mucous membrane which are present in the Ammocœte, persist in Petromyzon ; but, with the formation of a suctorial mouth, the portion of the œsophagus into which they open becomes closed posteriorly, and the œsophagus apparently grows forwards above the latter, and joins the mouth-cavity at the velum. Thus two canals pass backwards from the mouth, a ventral *branchial* or *respiratory tube*, and dorsal œsophagus (Fig. 220, B).

In Petromyzon and Bdellostoma [1] the individual branchial sacs, which communicate directly with the pharynx, open freely to the exterior : in Myxine this original condition becomes modified by the outer parts of the gill-passages growing out into long tubes, which

[1] In Bdellostoma there are usually six or seven pairs of branchial sacs, and behind these, on the left side, an *œsophageo-cutaneous duct* opens directly into the pharynx, as is also the case in Myxine. Bdellostoma polytrema possesses thirteen or fourteen pairs of gill-pouches.

unite to form a common duct on either side ; this opens far behind the branchial apparatus on the ventral side of the body.
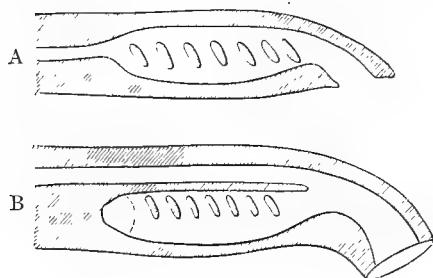


FIG. 220.—DIAGRAM OF A LONGITUDINAL SECTION THROUGH THE HEAD OF THE LARVAL (A) AND ADULT (B) *Petromyzon.*
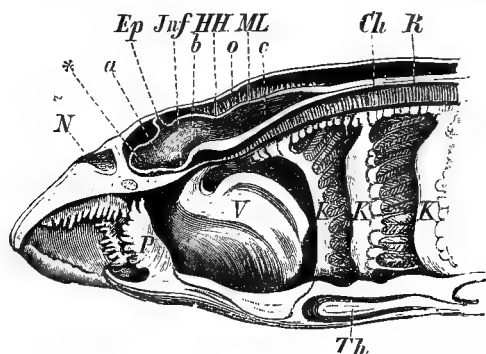


FIG. 221.—LONGITUDINAL SECTION THROUGH THE HEAD OF AN *Ammocœte.*

*V*, velum ; *P*, papillæ of mucous membrane ; *K, K, K*, three anterior gills ; *Th*, thyroid (hypobranchial furrow) ; *N*, nasal sac ; *, communication between the ventricle of the olfactory lobe and that of the prosencephalon ; *Ep*, epiphysis ; *Jnf*, infundibulum ; *HH*, metencephalon ; *Ml*, medulla oblongata ; *b, c*, ventricles of the mid- and hind-brain ; *o*, subdural cavity ; *Ch*, notochord ; *R*, spinal cord.

**Fishes.**—From the Elasmobranchii onwards, the gills are in close relation with the visceral skeleton, and in these Fishes they consist of closely-approximated transverse laminæ (Figs. 222 A, 223), which are firmly attached to both sides of the septa which separate the individual gill-sacs from one another, so that each septum bears a half-gill, or *hemibranch*, on both its anterior and posterior surface. A gill, or *holobranch*, thus consists of the branchial arch *plus* the posterior hemibranch of the sac in front of it and the anterior hemibranch of the following sac. The gill-sacs, of which there are commonly five,[1] open separately to the exterior, and a rudimentary

[1] There are six in Hexanchus and Chlamydoselache and seven in Heptanchus.

gill-cleft known as the *spiracle* (p. 75), is as a rule present more
anteriorly, between the mandibular and hyoid arches. In the Holo-
cephali, however, the spiracle becomes reduced, there are only three
holobranchs in addition to hemibranchs on the hyoid and fourth
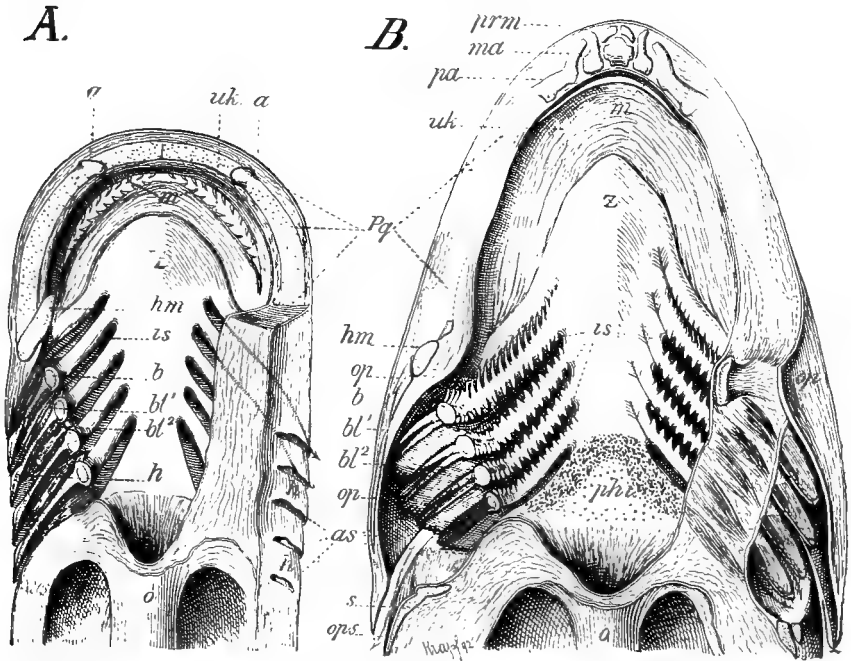


Fig. 222.—Dissection of the head from the ventral side of A, an Elasmobranch
(*Zygæna malleus*), and B, a Teleost (*Gadus aeglefinus*), to show the branchial
apparatus. In both figures the branchial arches on the left side are shown
cut through horizontally. (From R. Hertwig's *Zoology*.)

*Pq*, palatoquadrate, and *a*, its connection with the cranium anteriorly ; *uk*,
lower jaw ; *m*, oral cavity ; *prm*, premaxilla ; *ma*, maxilla ; *pa*, palatine ;
*hm*, hyomandibular ; *is*, internal branchial apertures ; *as*, external branchial
apertures ; *ops*, opercular aperture ; *h*, branchial septum ; *bl¹*, anterior, and *bl²*,
posterior hemibranch of a gill-pouch ; *op*, operculum ; *s*, pectoral arch ; *z*,
tongue ; *phi*, inferior pharyngeal bone ; *o*, œsophagus.

branchial arch, and an opercular membrane is present, covering the
external branchial apertures and opening by a slit posteriorly ;
traces of a similar structure are seen in Chlamydoselache.

In Ganoids and Teleosts there are no longer chambered gill-
sacs. The septa on which the gill-laminæ are borne become
greatly reduced, so that the apices of the latter extend freely out-
wards ; the whole branchial region is, moreover, covered over by the
operculum and branchiostegal membrane (comp. pp. 75 and 79),

and thus, as in the Holocephali, the gill-slits open into a common branchial chamber, which communicates with the exterior by a single slit-like aperture on either side (Figs. 222 B and 223). A spiracle is present in Acipenser, Polyodon, and Polypterus amongst Ganoids.

As a rule Teleosts possess only four holobranchs,[1] and this holds good for all Ganoids.

A rudimentary gill or *pseudobranch* is present on the anterior wall of the spiracle of many Elasmobranchs and of cartilaginous Ganoids (mandibular pseudobranch); and the posterior hyoid hemibranch, which is functional in Acipenser and Lepidosteus, becomes more or less reduced in Ganoids and Teleosts, forming the so-called opercular pseudobranch. Traces of a cleft, lying behind the functional branchial clefts, are found in the embryos of certain Elasmobranchs. All these facts indicate that Fishes formerly possessed a more extensive branchial apparatus than at present.

In the Lophobranchii the gills are replaced by tufted processes, and in many Teleostei certain accessory structures are developed in the region of the branchial chamber by a modification of the branchial arches or cavities. These serve to retain the water, and thus the Fish is able to live for some time out of the water (Anabas, Saccobranchus, Heterobranchus, Clarias).

External gills are met with in young stages of Elasmobranchii and Holocephali as well as in Polypterus and Calamoichthys; in Elasmobranchii and Holocephali, at any rate, they are *endodermal* and not ectodermal in origin.

Fishes breathe by taking in water through the mouth, and, by the contraction of the latter, forcing it out again through the gill-slits.[2] In this process the gill-arches rise and fall, separating from one another during inspiration, and approximating during expiration.

**Dipnoi.**—These, as their name implies, possess both gills and lungs, only the latter organs being functional in Protopterus during its summer sleep (see p. 17). Besides the internal gills, which are covered by a small operculum, Protopterus possesses three pairs of external gills situated just above the operculum and supplied by vessels from the arterial arches. In Ceratodus, in which, as in Lepidosiren, no external gills are present, there are four complete gills on the first four branchial arches, as well as a pseudobranch

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[1] They may be reduced to three, or two, and even these may become more or less rudimentary.

[2] In the Lamprey inspiration as well as expiration takes place through the gill apertures when the animal is attached by means of its suctorial mouth.

on the hyoid. In Protopterus and Lepidosiren a reduction of these organs has taken place, gills being absent in the former genus on the first and second branchial arches; there is, however, in addition, an anterior hemibranch on the fifth branchial arch.

**Amphibia.**—In the embryos of Urodeles, five gill-clefts can usually be recognised, but the most anterior and posterior of these do not become open to the exterior. In the larvæ, as well as in adult Perennibranchiates, there are three external gill-tufts in connection with the three anterior branchial arches, lying one over the other;
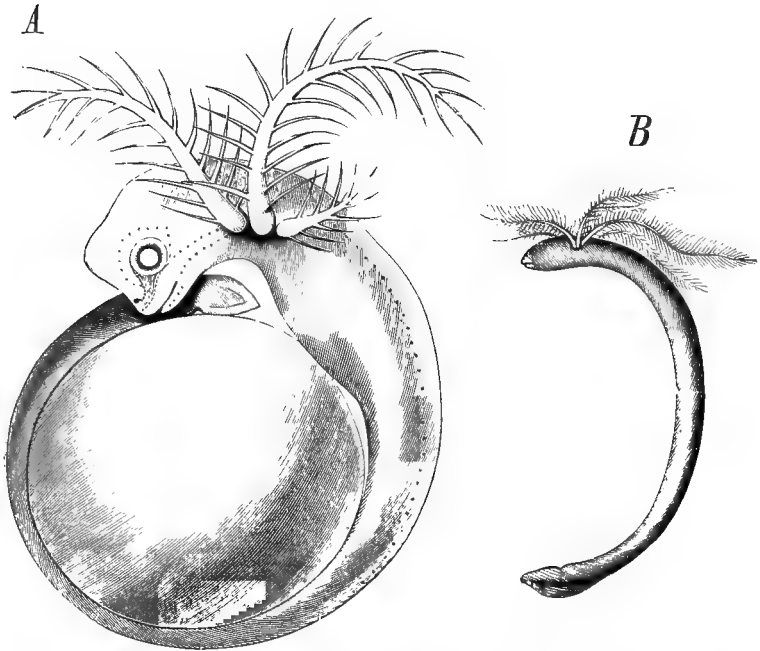


FIG. 224, A and B.—LARVA OF *Epicrium glutinosum*, WITH EXTERNAL GILLS. (After Sarasin.)

these extend backwards, projecting freely to the exterior, and are composed of connective-tissue, unsupported by cartilage. They either have the form of tufts, or may be delicately branched, showing the most varied arrangements for increasing the respiratory surface (comp. Fig. 224). These external gills are ectodermal in origin, and must not be confused with the internal gills, which are wanting in all Urodeles. They are acted on by a complicated system of muscles, and are covered by ciliated epithelium, which serves to keep up a continual current in the surrounding medium.

In the Axolotl and in larval Salamanders there are four, and in Necturus (Menobranchus) and Proteus only two gill-clefts perfora-

ting the pharynx. The former thus show a more primitive condition, while in the latter these structures have become reduced. There is always only a single external opening covered over by an opercular-like fold of skin.

The usually feather-like external gills present at first in Anura soon disappear, and their place is taken by internal gills, the epithelium covering which is also said to be ectodermal in origin. By the growth of the opercular folds, which contain no skeletal parts, the external respiratory aperture of either side becomes gradually reduced in size, and the two branchial chambers usually open eventually by a single aperture, which is situated either in the median ventral line, or laterally.

The larvæ of the Gymnophiona also possess external gills, which vary much in form in the different genera (Fig. 224).

In certain Batrachia in which there is no free larval stage it appears that respiration may take place before hatching in the broad and vascular tail (Hylodes martinicensis), in folds of the ventral body wall (Rana opisthodon), or in peculiarly modified external gills (Nototrema).

Except in the Perennibranchiata, the gills disappear at metamorphosis and the respiratory apertures close up. In the Derotremata, however, the gill cleft between the third and fourth branchial arches persists.

## II. AIR-BLADDER AND LUNGS.

### 1. THE AIR-BLADDER.

As already mentioned (p. 273), the lungs and swim-bladder are developed in a similar manner, and only differ from one another in the fact that the lungs always arise from the ventral side of the pharynx, while this is only exceptionally the case as regards the air-bladder (e.g., Polypterus, Calamoichthys), which usually arises on the dorsal side. The exact point of origin of the air-bladder from the alimentary canal varies,[1] and its duct (ductus pneumaticus) may either remain open throughout life, as in all Ganoids and some Teleosts (Physostomi), or it may later become reduced to a solid fibrous cord or even entirely obliterated, as in other Teleosts (Physoclisti). In the latter case there is no communication between the swim-bladder and the external air, and it is probable that the contained gas is given off from the walls of the swim-bladder itself. A vascular organ (the so-called "rete mirabile"), consisting of numerous glands and capillaries, is present in the walls of the swim-bladder in the Physoclisti, and in certain Physostomi a

[1] In Erythrinus it arises laterally, and in some Physostomi (e.g., Herring) it opens further back into the stomach.

somewhat similar organ ("red-body") is present, but consists of capillaries only.

The air-bladder lies above the peritoneum on the dorsal side of the body-cavity, between the vertebral column, aorta, and kidneys on the one hand, and the alimentary canal on the other : it is invested by the peritoneum on the ventral side only. It is more or less sac-like in form, and is only exceptionally paired (Polypterus); it usually extends along the whole length of the body-cavity, and its walls are composed of connective, elastic, and muscular tissue. In some Teleostei it is transversely constricted so as to form several successive divisions; in other cases it may give rise to a more or less numerous series of cæcal processes.[1] Its internal surface may be either smooth or spongy (Fig. 225) owing to the formation of a meshwork of trabeculæ, the structure of which resembles that of the lungs of



FIG. 225.—INTERNAL SURFACE OF THE AIR-BLADDER OF LEPIDOSTEUS, SHOWING THE TRABECULÆ.

*B*, fibrous longitudinal band.

Dipnoi and Amphibia, and as already stated, it has a respiratory function in some cases.

An air-bladder is wanting in Cyclostomes and Elasmobranchs.

Attention has already been directed to the relations which often exist between the air-bladder and the auditory organ (see p. 226).

## 2. THE LUNGS.

The lungs arise at the hinder border of the branchial region of the pharynx, which here becomes divided by a longitudinal horizontal fold into a dorsal and a ventral portion, the latter of which gives rise to a blind sac, opening anteriorly by a wide aperture into the former and composed of endoderm surrounded by mesoderm (Fig. 226). A longitudinal vertical furrow is then formed, dividing this primitive lung-sac into right and left halves : the narrower proximal portions of these represent the primitive *bronchi*, which communicate with the pharynx by a single tube, the primitive windpipe or *trachea*. The proximal end of the latter usually becomes differentiated to form a *larynx*, or organ of voice, which opens into the pharynx on its ventral side by means of a slit-like aperture, the *glottis*. The lungs are therefore phylogenetically older organs than

[1] In the Gymnodonts (*e.g.*, Diodon, Tetrodon), the whole œsophagus is capable of great distension.

the bronchi, trachea, and larynx, and this statement is supported by a study of their comparative anatomy.
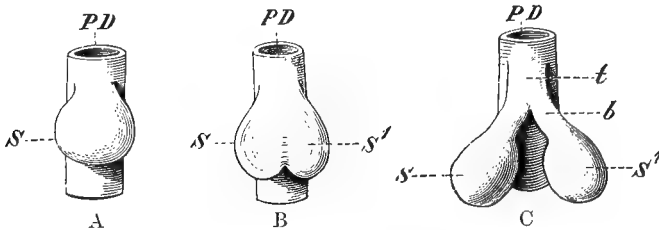


FIG. 226.—A, B, C, DIAGRAMS SHOWING THE MODE OF DEVELOPMENT OF THE LUNGS.

*PD*, primitive alimentary tube ; *S*, *S*[1], the lung-sacs, which are at first unpaired ; *t*, trachea ; *b*, bronchus.
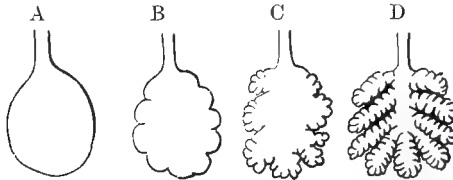


FIG. 227.—DIAGRAM ILLUSTRATING THE PHYLOGENETIC DEVELOPMENT OF THE LUNGS ; A GRADUAL INCREASE OF THE RESPIRATORY SURFACE IS SEEN IN PASSING FROM A TO D.

Hollow outgrowths and buds arise from the endoderm of the lungs and extend into the surrounding vascular mesoderm, which
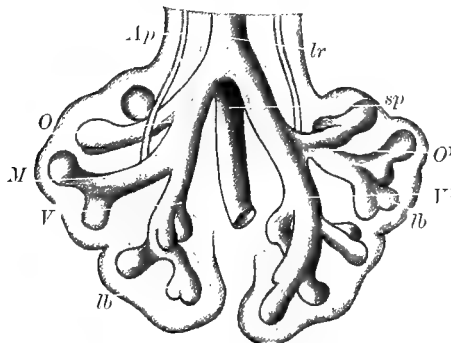


FIG. 228.—DIAGRAM OF THE EMBRYONIC HUMAN LUNG. (After W. His.)

*Ap*, pulmonary artery ; *lr*, air-passage ; *sp*, œsophagus ; *lb*, pulmonary vesicle undergoing division ; *O*, right upper (anterior) lobe of the lung with its eparterial bronchus ; *M*, *V*, middle and lower (posterior) lobes ; *O*[1], left upper lobe with its hyparterial bronchus ; *V*[1], left lower lobe.

gives rise to muscular fibres and connective-tissue, and thus a branched system of cavities communicating with the bronchi is

gradually formed (secondary and tertiary bronchi). The ends of these branches are swollen, forming vesicles known as *infundibula*, which are made up of a number of *alveoli*, and are surrounded by blood capillaries, through the thin walls of which the interchange of respiratory gases takes place (Figs. 227 and 228).

In the following account the air-tubes will be dealt with separately from the lungs proper.

### Air-Tubes and Larynx.

The walls of the air-tubes may consist, in addition to their lining of ciliated epithelium, of connective-tissue and elastic and muscular fibres only, but usually cartilaginous elements are also formed, and these serve to keep the tubes permanently open. The most anterior of these cartilages, which support the larynx, become differentiated to form a frame on which the structures by means of which the voice is produced—the *vocal cords*,—are stretched : these cartilages are acted upon by muscles. The relative length of the windpipe, as a rule, corresponds with that of the neck.

**Dipnoi.**—In these the glottis is supported by a fibro-cartilage, and leads into a muscular vestibule communicating with the lung. A larynx and trachea are not differentiated.

**Amphibia.**—The vestibule, or *laryngo-tracheal chamber*, communicates with the pharynx on the one hand and with the lungs on the other, and is supported by cartilages : it is provided with intrinsic (dilator and constrictor) and extrinsic muscles, the former derived from pharyngeal muscles and the latter from trunk muscles. A definite trachea is differentiated in Siren, Amphiuma, and the Gymnophiona only ; it reaches a length of 4 to 5 or more centimetres, and its wall is strengthened by a series of small irregular cartilages, which usually tend to unite into bands (Fig. 229): only in the Gymnophiona, however, do these bands begin to take on the form of half-rings, and to surround the trachea more or less completely.

The phyletically oldest skeletal parts are a pair of *arytenoid cartilages*, situated in the walls of the vestibule (Fig. 229): these appear to have arisen by a modification of part of the fifth branchial arch (comp. Fig. 233). Distally to them there is, in the Anura, another cartilage corresponding to the *cricoid* of higher forms, and traces of this also occur amongst Urodeles (*e.g.*, Siren).

In Anura a highly differentiated larynx is present. This is regulated by a well-developed series of muscles, and is provided with *vocal cords*, the sound produced by which is often intensified by the presence of vocal sacs developed from the floor of the mouth. The laryngo-tracheal chamber lies between the posterior cornua of the hyoid (thyro-hyals) and is supported by a thin arytenoid cartilage

on either side of the glottis as well as by a ring-shaped cricoid cartilage, from which delicate processes pass backwards to the



FIG. 229.—LARYNGEAL AND TRACHEAL SKELETON OF URODELES. A, *Necturus* (*Menobranchus*) ; B, *Siren lacertina* ; C, *Amphiuma* ; D, *Salamandra maculosa*.

*a*, the cartilages (arytenoids) on either side of the glottis ; *a'*, ridge for muscles ; \*, the representative of the cricoid cartilage ; ††, cartilages of the trachea in Siren ; *Kb*, the more definite tracheal cartilaginous tracts in Amphiuma and Salamandra ; *K*$^{IV}$, fourth branchial arch, from which the dilator (*d*) of the trachea and larynx arises ; *co*, constrictor of the larynx ; *L*, *L'*, lungs.

roots of the lungs (Fig. 230). Vocal cords are developed in the Anura only, each being attached to the inner concave surface of the corresponding arytenoid.



FIG. 230.—CARTILAGINOUS SKELETON OF THE LARYNGO-TRACHEAL CHAMBER OF *Rana esculenta*. (A, from above ; B, from the side.)

*Ca, Ca*, arytenoid cartilage ; *C.l.*$^{1}$ to *C.l.*$^{4}$, cricoid cartilage ; *Sp*, process of the latter ; *P*, plate-like broadening out of the ventral part of the cricoid ; *SR*, glottis ; \*\*\*, three tooth-like prominences of the arytenoids.

**Reptiles.**—The larynx of Reptiles is supported by cartilaginous elements comparable to those of Anura, there being two sets of

cartilages—a paired arytenoid, and a ring-shaped cricoid (Figs. 76 and 231). No considerable advance in structure is seen ; there is even a reduction noticeable as regards the musculature as compared with the Anura.

One point, however, must be specially noticed, viz., the close connection which obtains between the larynx and the hyoidean
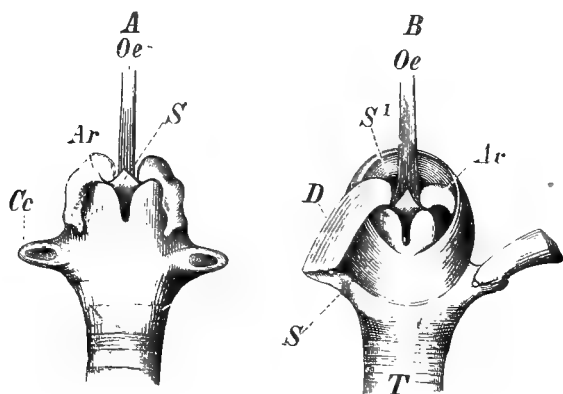


Fig. 231.—Larynx of *Phyllodactylus europæus.* (A, skeleton, and B, musculature of larynx.)

*Ar*, arytenoids ; *Cc*, cricoid ; *S*, anterior median process of cricoid ; *S¹*, sphincter ; *D*, dilator ; *T*, trachea ; *Oe*, basi-hyal.

apparatus—more particularly the dorsal surface of the basi-hyal. In Crocodiles and Chelonians, for instance, the larynx is firmly embedded in a shallow depression of the latter (Fig. 76).

A well-developed trachea, supported by cartilages, is present in all Reptiles ; but the cartilages are not in all cases fused together to form complete rings. The walls of the bronchi are also usually provided with cartilaginous supports.

**Birds.**—In Birds there are two larynges, an *upper* and a *lower*. The former lies in the usual position behind the tongue on the floor of the pharynx, and is plainly homologous with that of other Vertebrates, though it has become rudimentary and is incapable of producing sound.

The lower larynx, or *syrinx,* is of much greater importance ; it is usually situated at the junction of the trachea and bronchi, or more seldom at the lower end of the trachea alone or on the bronchi alone. It functions as the organ of voice, and appears first in, and is restricted to, Birds. In the most usual form (*broncho-tracheal syrinx*), there is a movable connection between the most anterior bronchial rings, with which a complicated system of muscles is connected ; these, by their contraction, cause a stretching or relaxing of

certain vibratory membranes. A bar of cartilage or bone, the *pessulus*, extends from the junction of the bronchi into the more or less swollen "*tympanum*" at the base of the trachea: this supports a slight fold of the mucous membrane called the *membrana semilunaris*, while the membranous inner wall of each bronchus is known as the *membrana tympaniformis interna*: the external wall may also give rise to a *membrana tympaniformis externa*. The
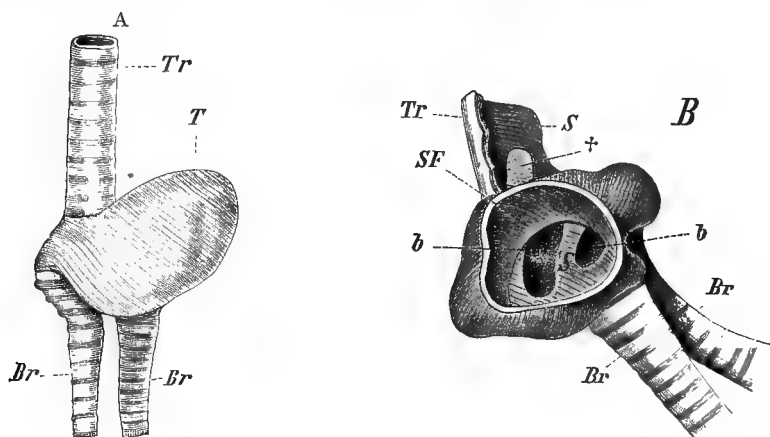


FIG. 232.—LARYNX OF MALE DUCK.  (*A*, external, and *B*, internal view.)

*Tr*, trachea; *Br*, bronchus; *T*, the "tympanum"; *S*, pessulus, from which a lateral outgrowth (*S* between *b* and *b*) extends into the tympanum, thus dividing its aperture into the trachea into two portions (*b*, *b*); the aperture is further diminished by the circular fold of mucous membrane, *SF*; †, thin region in *S*.

tympanum attains a relatively enormous development in some Water-Birds (*e.g.*, the male Duck), where it gives rise to a bony vesicle which serves as a resonance cavity (Fig. 232).

The length of the trachea in Birds varies greatly, and its complete cartilaginous rings usually become ossified. In some cases (*e.g.*, the Swan and Crane) it extends into the hollow keel of the sternum, where it becomes more or less coiled, and then again passes out close to its point of entrance and enters the body-cavity. In certain representatives of the Sturnidæ it extends between the skin and the muscles of the thorax, and there gives rise to numerous spiral coils.

**Mammals.**—The larynx of Mammals is distinguished from that of all other Vertebrates by the marked differentiation of the muscles—the constrictors always exceeding the dilators in number —and by the constant presence of an *epiglottis* and a *thyroid cartilage*.

The thyroid cartilage is derived from part of the fourth and fifth branchial arches (comp. Fig. 233), and in Monotremes, in which it is paired, it is still closely connected with the hyoid apparatus

(comp. p. 285). In all other Mammals the thyroid is unpaired, though still showing traces of its primary paired nature, and it becomes
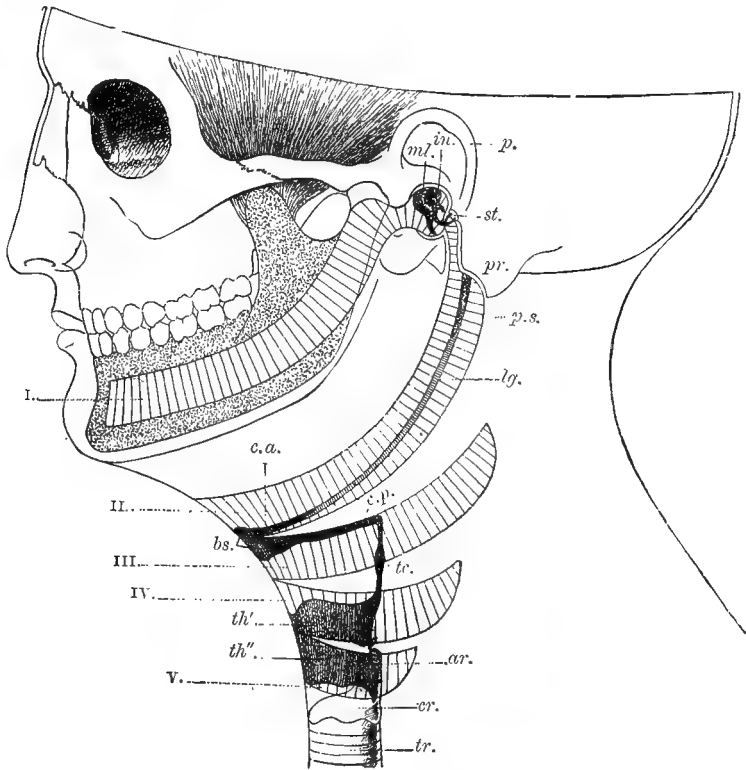


FIG. 233.—DIAGRAM TO ILLUSTRATE THE METAMORPHOSIS DURING DEVELOP-MENT OF THE FIRST TO FIFTH VISCERAL SKELETAL ARCHES (I—V) IN MAN.

From the proximal end of the first arch (Meckel's cartilage) two of the auditory ossicles, the malleus and incus (*mb* and *in*) are represented as arising. *p*, pinna; *pr*, mastoid process of skull.

From the second arch (hyoid) arise proximally the styloid process (*p.s*), distally the anterior (lesser) cornu of the hyoid (*c.a*) and a portion of the basi-hyoid (*b.s*). By far the greater portion of this arch becomes the stylo-hyoid ligament (*l.g*). (Concerning the stapes (*st*) comp., p 101).

The third (first branchial) arch gives rise to the greater part of the body (*b.s*) and the posterior or greater cornu of the hyoid (*c.p.*).

The fourth (second branchial) arch gives rise to the upper segment (*th'*) of the thyroid cartilage, and the fifth (third branchial) to the lower one (*th"*). The arytenoid cartilage (*ar*) is probably a derivative of the fifth arch. *tc*, cartilago triticea; *cr*, cricoid cartilage; *tr*, trachea.

separated from the hyoid: it is shield-shaped, and surrounds the lateral and ventral regions of the larynx, overlapping the cricoid

above,[1] and serving as a point of origin and insertion for important intrinsic and extrinsic muscles.

The vocal cords extend between the thyroid and the arytenoids, and the mucous membrane above them becomes involuted to form the laryngeal pouches.    In Anthropoids and certain other Monkeys (*e.g.*, Mycetes) these may reach such a large size that they serve as resonance cavities, and lie partially within the body of the hyoid, which is swollen to form a large bony chamber (Fig. 234). The folds of mucous membrane bounding the laryngeal pouches anteriorly are spoken of as false vocal cords ; these are not present in all Mammals.

The epiglottis, which consists of elastic fibro-cartilage, stands in close relation to the soft palate, extending upwards from the anterior border of the larynx, in front of the glottis : it is often, when at rest, embraced more or less firmly by the soft palate in such a way that its distal end lies in the passage of the posterior nostrils (naso-pharyngeal chamber), so that respiration and feeding can go on independently of one another.[2]

An interesting adaptation for the method of lactation is seen in the larynx of Marsupial embryos, in which it, together with the epiglottis, becomes greatly elongated and is firmly embraced by the soft palate, so that it cannot be moved from this position. Thus respiration can go on freely while the milk passes down the oesophagus on either side of the larynx. In Cetecea (*e.g.*, Phocæna), a similar arrangement occurs, and is here adapted for the aquatic life of the animal.    Probably in all Mammals a similar position of the larynx is seen in the embryo.

## The Lungs proper.

**Dipnoi.**—In Ceratodus the lung is a wide unpaired sac, without any trace of a dividing septum : in other Dipnoans it is distinctly paired throughout the greater part of its length, the anterior unpaired portion being largely filled up by spongy trabeculæ.

The lung extends through the whole length of the body-cavity, and is covered by peritoneum on the ventral surface only ; the lining mucous membrane forms bands and networks similar to those seen in the air-bladder of many Fishes (*e.g.*, Lepidosteus, Fig. 225).

**Amphibia.**—The lungs of Proteus and Necturus (Fig 235), though paired throughout, remain at a lower stage than those of the Dipnoi, inasmuch as their internal surface is perfectly smooth, and has, therefore, a much smaller superficial extent.    They

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[1] The cricoid may be complete or incomplete ventrally, and its dorsal portion usually becomes raised to form a broad plate with which the arytenoids are articulated (Figs. 233 and 234).

[2] The epiglottis was probably originally a paired structure, consisting of hyaline cartilage, and it is possible that the small cartilages of Wrisberg and Santorini present in the larynx in addition to the more important cartilages described above may be specialisations of part of the same structure.
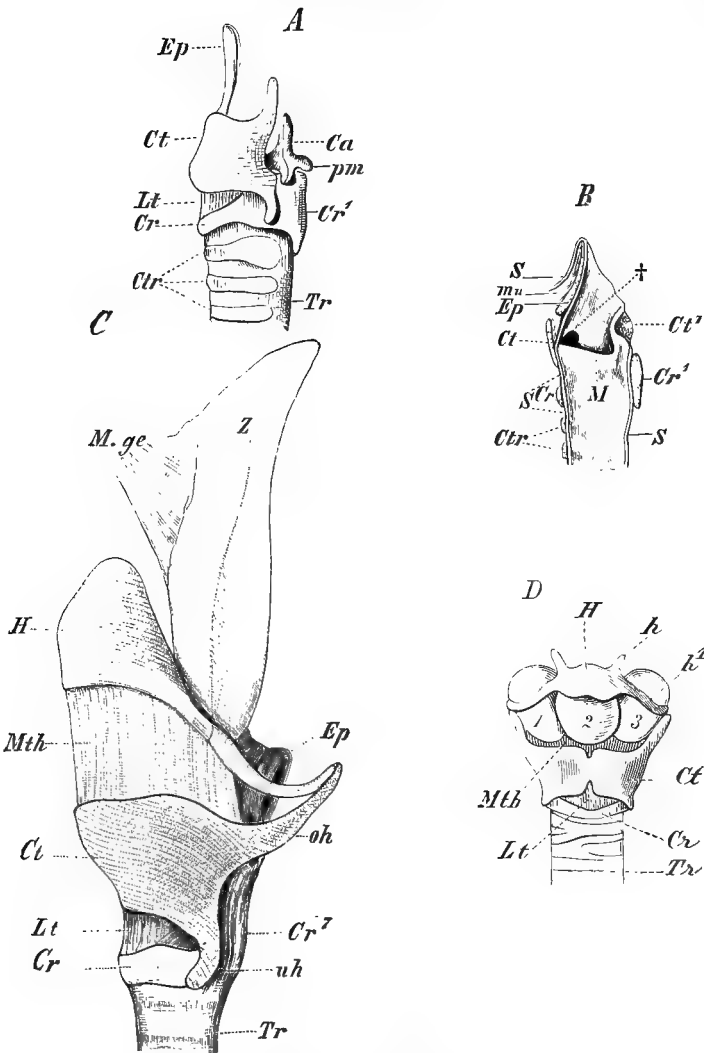
FIG. 234.—LARYNGES OF VARIOUS MAMMALS.

A, larynx of Deer, seen from the left side ; B, longitudinal section through the
larynx of the Fox ; C, larynx of the Howling Monkey (*Mycetes ursinus*), from
the left side ; D, Larynx of Chipanzee (*Simia troglodytes*), from the ventral
side.

*Tr*, trachea ; *Ctr*, cartilaginous rings of the trachea ; *S*, mucous membrane of the
trachea and tongue ; *Cr*, ventral, and *Cr*¹, dorsal plate of the cricoid ; *Ct*,
*Ct*¹, thyroid cartilage ; *oh*, *uh*, anterior and posterior cornua of the latter ;
*Ca*, arytenoid cartilage ; *pm*, processus muscularis of the latter ; *Ep*, epi-
glottis ; *H*. body of hyoid ; *h*, lesser, *h*¹, greater cornua of the hyoid ; *Lt*,
crico-thyroid ligament ; *Mth*, thyro-hyoid ligament ; *M*, laryngeal pouch,
which shows an enlargement at †; *1, 2, 3*, the three resonance cavities of
*Simia troglodytes* ; *mu*, submucous tissue with muscles ; *M.ge*, genioglossus
muscle ; *Z*, tongue.

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consist of two delicate elongated sacs of unequal length, and constricted in the middle; in Proteus they extend much further backwards than in Necturus. A difference in length between the two lungs is seen also in other Amphibia, such as Amphiuma and Siren, in which the two cylindrical lungs lie near together, close to the aorta. Their internal surface is raised into a network, corresponding with the distribution of the blood-vessels, the meshes being much finer in Amphiuma, and still more so in Menopoma, than in Siren.

In many Salamanders (*e.g.*, Salamandrinæ, Amblystomatinæ, Desmognathinæ, Plethodontinæ) the lungs undergo a more or less complete degeneration, even though all traces of the gills disappear. The fact that the floor of the mouth is continually raised and lowered as in other Amphibians which possess lungs, and that in some cases, at any rate, the animal dies if these respiratory movements are prevented, indicates that a bucco-pharyngeal respiration takes place, and that cutaneous respiration (which occurs in most Amphibians) alone is insufficient. In other Salamanders the lungs are as a rule equal in size, and have the form of cylindrical tubes extending backwards as far as the end of the stomach; their internal surface is more or less smooth. The lungs of the Gymnophiona are similar to those of Salamanders, but the right alone is fully developed, and this shows in its interior a complicated trabecular network: the left is only a few millimetres long.

FIG. 235.—LUNGS OF PROTEUS (A) AND NECTURUS (B). The communication with the vestibule is indicated by a black spot anteriorly.

The sac-like lungs of Anura are quite symmetrical. Their internal surface, which is lined partly by ciliated epithelium, is raised up into a rich respiratory network of trabeculæ, and numerous smooth muscular fibres are present in their walls.

**Reptiles.**—In Reptiles, as in all other air-breathing Vertebrates, the form of the lungs is to a great extent regulated by that of the body. In the higher types, such as the Chelonia and Crocodilia, their structure is much more complicated than in Amphibia; this complication finds expression in a very considerable increase of the respiratory surface. With the exception of the thin-walled lungs of Lizards, which retain a very primitive condition, we no longer meet with a large central cavity, but the organ becomes penetrated by a branched system of bronchi, which

give rise to a tubular and sponge-like meshwork (comp. Fig. 236).

The lung of Snakes exhibits an intermediate form, for in spite of the finely-meshed tissue arising from the periphery, it still retains a narrow central cavity.   The right lung only is as a rule fully developed in Snakes and Amphisbœnians, owing to the elongated form of the body, while the left remains in a rudimentary condition, or even disappears entirely.

In the Chameleon (Fig. 236) the anterior portion of the lungs is much more compact and spongy than the posterior, which grows out into numerous sac-like processes, some of which reach as far back as the pelvic region ; their form is very variable, being spindle-shaped, club-shaped, or lobulated, and their walls are very thin ; they extend in amongst the viscera wherever there is room.   If these processes have any respiratory function, it is at most only a very slight one.   An indication of a similar arrangement is seen in the lungs of Testudo, in which a single thin-walled process extends backwards to the pelvic region.   These processes seem to foreshadow a condition which reaches its highest development in Birds.

A uniform ground-plan is to be observed in the arrangement of the intra-pulmonary bronchial system through the whole series of the Amniota, from Crocodiles onwards. A continuation of the bronchus, which is almost straight, always passes through the lung to its posterior end.   This may be called the *main bronchus ;* from it a series of *lateral bronchi* arise.

**Birds.**—The respiratory apparatus of Birds presents so many -remarkable peculiarities, both as regards the structure of the lungs



Fig. 236.—LUNGS OF *Chamæleo monachus.*

*T*—trachea.

and in the presence of *air-sacs,* that it must be considered in some detail.

The comparatively small but highly vascular lungs (Figs. 237 and 238) are closely applied to the thoracic vertebræ and heads of

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the ribs, and are capable of very little distension.  They are pene-
trated by a system of bronchi which will be described presently.
The lower surface of each lung is closely invested by a thin fibrous
membrane, the *pulmonary aponeurosis*,[1] into which are inserted a
variable number of muscular bands (*costo-pulmonary muscles*):
these arise from the vertebral ribs, and are supplied by the inter-
costal nerves (Fig. 238).

When the ventral body-wall of a Bird is removed, the heart,
stomach, liver, and intestine are seen pressed towards the mid-line,
and on either side of them a tightly-stretched fascia, the *oblique
septum,* is observable, which shuts them off from a paired lateral
*sub-pulmonary chamber* (Fig. 237).  Other chambers are situated
in the anterior thoracic region, ventral to the lungs.  Others, again,
are seen in the region of the heart and in the posterior part of the
abdominal cavity.  These chambers are occupied by the *air-sacs*
with which certain of the bronchi communicate.

The most posterior chamber on either side encloses an *abdominal
(posterior)* air-sac (Fig. 237).  In Apteryx, this is completely closed in by
the oblique septum, but in other Birds it gives rise to a large, distensible
diverticulum which extends backwards ventrally to the kidney, amongst the
viscera.

In front of this there are two air-sacs lying above and externally to the
oblique septum, and constituting the main part of the sub-pulmonary
chamber ; these may be called the *anterior* and *posterior intermediate* sacs.
A transverse dividing-wall separates these, at the level of the cœliac
artery, and a second septum shuts off the anterior intermediate sac from the
one lying in front of it, to be described presently.  The posterior inter-
mediate air-sac presents the simplest and most constant relations, and never
communicates with any of the neighbouring chambers, as is often the case
with the anterior intermediate.

A pair of *prebronchial* air-sacs lies on either side of the œsophagus above
each bronchus, anterior to the hilum of the lung, and below this a *sub-bronchial*
sac is situated, which is separated behind from the anterior intermediate sac
by a septum.   This is usually unpaired, the sac of either side fusing with its
fellow to form an *interclavicular* chamber, bounded by the furcula [2] ; it com-
municates with neighbouring air-cavities which lie between the pericardium
and sternum and in the axilla, outside the body-cavity (*axillary* sac).

The *main bronchus (mesobronchium)* runs close to the ventral surface of
the lung surrounded by the lung-parenchyma, and extends to its posterior
end, where, as a rule, it opens directly into the abdominal air-sac (Fig. 238).
From it a large *lateral bronchus* is given off, which opens into the posterior
intermediate sac by one or two (*e.g.*, in Passeres) apertures.  Besides this
there are from four to six other lateral bronchi, all of which become
broadened out in a fan-like manner on the ventral surface of the lung.
These may be called *entobronchia* (*bronchi divergentes*) : they all arise from
the anterior portion of the mesobronchium.   The first of these radiates out

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[1] The pulmonary aponeurosis, as well as the oblique septum, is often spoken of
as a "diaphragm" (comp. p. 141).   The chamber (pleural cavity) in which the
lungs are situated is shut off from the rest of the abdominal cavity in Chelonians
and Crocodiles also.

[2] In some Birds (*e.g.*, Rhea, Vulture, Adjutant) a median septum is present
separating the two sub-bronchial sacs.
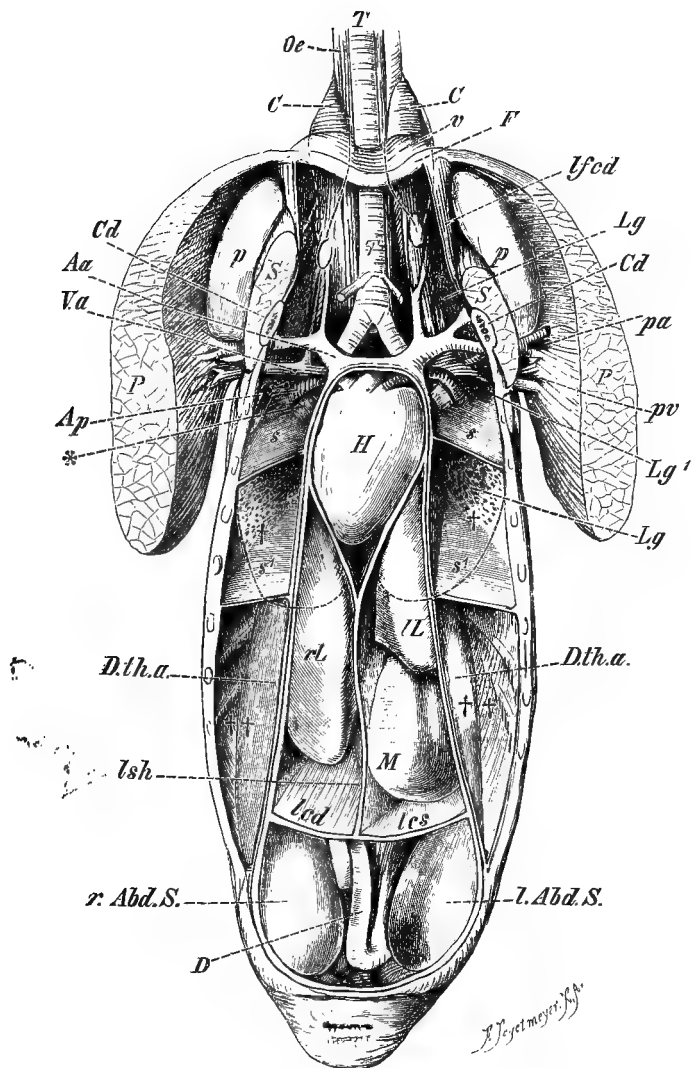
FIG. 237.—ABDOMINAL VISCERA AND AIR-SACS OF A DUCK AFTER THE RE-
MOVAL OF THE VENTRAL BODY-WALL. (From a drawing by H. Strasser.)

T, trachea ; H, heart, enclosed within the pericardium ; rL,lL, right and left
lobes of liver ; lsh, suspensory (falciform) ligament, and lcd, lcs, right and
left coronary ligament of the liver ; D, intestine ; P, pectoralis major ; pa,
pv, pectoral artery and vein ; S, subclavius muscle ; Cd, coracoid ; F, furcula ;
lfcd, coraco-furcular ligament ; Lg, Lg¹, lung ; r.abd.S, l.abd.S, right and
left abdominal (posterior) air-sac ; D.th.a, oblique septum ; ††, posterior
intermediate air sac ; †, anterior intermediate air-sac ; s¹, s¹, partition-walls
between these sacs ; s, s, partition walls between the anterior intermediate
air-sacs and the unpaired sub-bronchial sac, lying in the anterior part of the
body-cavity ; v, portion of anterior wall of latter ; p, axillary sac lying
between the coracoid, scapula, and the anterior ribs, and communicating with
the sub-bronchial air-sac ; C, C, prebronchial sacs ; *, point of entrance of
the bronchi into the lung ; Ap, pulmonary artery ; Aa, Va, innominate artery
and vein with their branches.
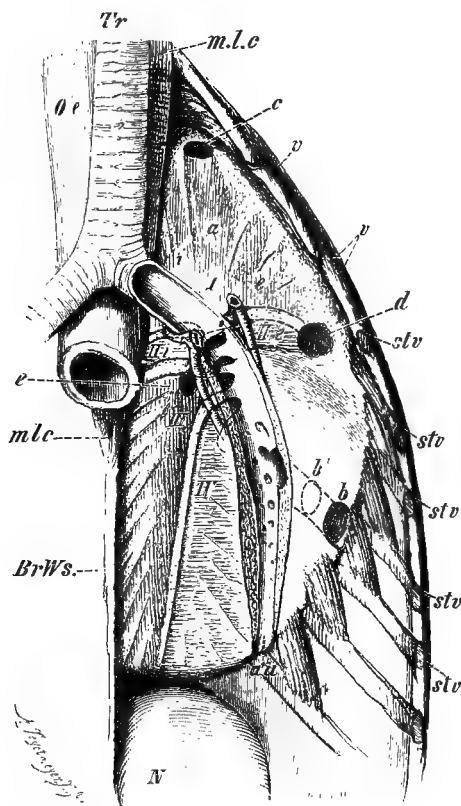
Fig. 238.—Left Lung of the Duck, *in situ*. (From a drawing by H. Strasser. The main bronchus is cut open; internally to it lies the pulmonary vein, and externally the pulmonary artery.

*Oe*, œsophagus; *m.l.c*, musc. longus colli; *Br.Ws*, thoracic vertebræ; *r*, *r*, ends of free vertebral ribs; *stv*, *stv*, sections of ribs which are connected with the sternum; *N*, kidney; *Tr*, trachea, *I*, first entobronchium, and *c*, its ostium communicating with the prebronchial air-sac; *i*, *a*, *e*, its internal, anterior, and external branches; *IIi*, *IIe*, internal and external branch of the second entobronchium : the end of *IIe* opens into the sub-bronchial sac at *d*; *III*, third entobronchium, with the aperture for the anterior intermediate air-sac; *IV*, fourth entobronchium; *au*, opening of the main bronchus into the abdominal sac; *b*, opening of the outer lateral branch of the mesobronchium into the posterior intermediate air-sac; *b¹*, second ostium of the latter, more towards the middle line (present in Passeres). The boundary of the pulmonary aponeurosis is seen along the outer edge of the lung, and the costopulmonary muscles are shown extending from it to the ribs.

anteriorly to the hilum of the lung, and gives off internal, external and anterior branches, one of which opens into the prebronchial sac. The other entobronchia give rise to two series of branches, one of which extends inwards and backwards between the factors of the pulmonary vein, and the other outwards between the arterial branches. Almost without exception a large aperture or ostium is present on the wall on the third entobronchium,

communicating with the anterior intermediate air-sac.   A branch of the
second entobronchium opens externally to the hilum of the lung into the
sub-bronchial sac.

The lateral bronchi considered as yet have to do with the ventral surface
of the lung only ; but besides these there are a variable number of *ecto-
bronchia* arising from the dorsal side of the main bronchus posteriorly to the
entobronchia.   These come off in a longitudinal row, those of the outer row
being larger than those of the inner.   They pass dorsally to the costal face
of the lung.   Both ecto- and entobronchia give off numerous bronchi of a
third order, or *parabronchia* : the walls of these are raised into numerous
transverse net-like folds, into which the pulmonary capillaries extend.

The air-sacs arise from the embryonic pulmonary vesicles as
delicate-walled hollow processes, lined by pavement epithelium: these
grow rapidly, and soon exceed the lung proper in size, extending
amongst the viscera.   Their form and extent depend largely upon
their surroundings : they consist simply of interstitial cavities lined
by the membrane of the air-sacs.   Moreover, they are not confined
to the body-cavity, but in numerous places extend beyond it, pass-
ing in between the muscles, beneath the skin, and even into most
of the bones.   The latter are thus rendered *pneumatic*, and con-
sequently the specific gravity of the body is lessened, and the power
of flight increased.   The pneumaticity of the bones is not, however,
an essential peculiarity connected with flight, for in many Birds
which are extremely good fliers (*e.g.*, Larus, Sterna) the bones are
not pneumatic.[1]   In these cases, however, a compensation is
effected by a more marked development of the muscles, and the
abdominal (posterior) air-sac, which in no Birds appears to be
entirely wanting, is here well developed.   In the cursorial Ratitæ,
on the other hand, the bones are markedly pneumatic.

The air-sacs must be looked upon as integral parts of the
respiratory apparatus : a greater amount of air can, by their means,
pass in and out during inspiration and expiration, especially through
the larger bronchi, and consequently there is less necessity for the
expansion of the lung-parenchyma.   The function of the prolonga-
tions of the air-sacs lying towards the outer surface of the body
consists in the giving off of watery vapour and in regulating the
heat of the body.   Those which extend in between the muscles,
and supplant the connective and fatty tissue in these regions, have
a further importance in causing less power to be lost in friction.

But by far the greatest importance of the air-sacs situated towards
the periphery consists in the enlargement of the anterior thoracic
region, principally that surrounded by the pectoral arch.   A larger
development of the skeleton can thus take place, giving an increase

[1] The pneumaticity of the bones is not a special peculiarity of Birds : amongs
Mammals, frontal, maxillary, and sphenoidal sinuses are present in Anthropoids
Elephants, and Marsupials for instance ; the skull of Crocodiles is also strongly
pneumatic.   All these sinuses communicate with one another, and also with the
tympanic cavity.   They are in many cases developed in order to give a greater
surface for the attachment of muscles, and also to effect a saving of material and
a lightening of the skull.

of surface for muscular attachment without any considerable increase in weight. Everything, in fact, combines to establish an organ of flight with a large wing-surface and an increased strength of the muscles.

**Mammals.**—As in Reptiles, the blood-vessels are of fundamental importance in determining the structure of the bronchial system. The pulmonary artery crosses the main bronchus formed by the bifurcation of the trachea at its anterior end, and this point may be taken as dividing the lateral bronchi into two systems—an anterior *eparterial* and a posterior *hyparterial*.

The hyparterial series is always well developed, and consists of a double row of lateral bronchi, between the roots of which the pulmonary artery passes backwards dorsally, while the corresponding vein runs along the median side of the main bronchus (Fig. 239). The eparterial system, on the other hand, gradually becomes of much less importance and in certain cases is represented only by a single external lateral bronchus on either side (Fig. 239) ; and, as a rule, even the left of these disappears, only the right remaining, and even this is not always retained. The eparterial bronchus, whether developed on one or on both sides, may arise from the trachea instead of from the main bronchus.



Fɪɢ. 239.—Dɪᴀɢʀᴀᴍ ᴏꜰ ᴛʜᴇ Aʀ-
ʀᴀɴɢᴇᴍᴇɴᴛ ᴏꜰ ᴛʜᴇ Bʀᴏɴᴄʜɪ
ɪɴ Mᴀᴍᴍᴀʟs. (From the ven-
tral side.)

*a, a*, eparterial bronchus of either
side ; *b*, series of ventral, and
*c* of dorsal hyparterial bronchi ;
*A*, pulmonary artery ; *V*, pul-
monary vein.

In by far the greater number of Mammals, then, the left eparterial bronchus has disappeared, while the right is retained ; and as, therefore, the anterior lobe of the right lung belongs to the eparterial and that of the left lung to the first hyparterial bronchus, these lobes are evidently not homologous, the middle right lobe corresponding much more nearly to the anterior lobe of the left side. There is thus a want of symmetry between the right and left sides, the right lung usually retaining one more element than the left (Fig. 240ᴀ). The so-called accessory fourth lobe does not correspond to a true lobe, but represents the main axis of the lung enclosing the main bronchus.

The cartilages of the bronchi become more and more sparse and finally disappear as the latter divide up into finer and finer branches.

The thoracic cavity is lined by a serous membrane, the *pleura*, in which, as in the case of the peritoneum (p. 235), a *parietal* and
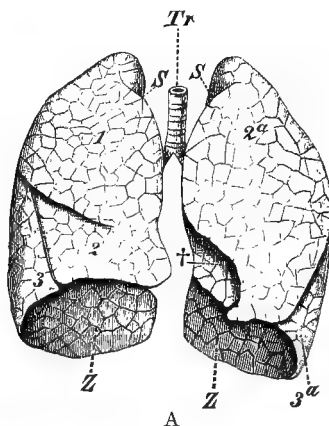


Fig. 240A.—Lung of Man.   (From the ventral side.)

1, 2, 3, lobes of the right, and 2*a*, 3*a*, of the left lung ; *Z*, base of lung ; †, incisura cordis ; *S*, sulcus for the subclavian artery ; *Tr*, trachea.
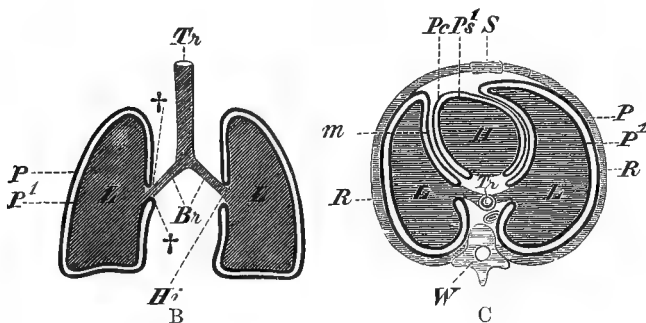


Fig. 240b and c.—Diagram of the Pleural and Pericardial Cavities of Mammals, founded on the Relations of these Parts in Man.  (B, horizontal section ; C, transverse section.)

*Tr*, trachea ; *Br*, bronchi ; *L, L*, lungs ; *H*, heart ; *W*, vertebral column ; *P*, parietal, and *P¹*, visceral layer of the pleura ; ††, points at which these pass into one another at the hilum pulmonalis (*Hi*) ; *m*, mediastinum ; *Pc, Ps¹*, parietal and visceral layers of the pericardium ; *R*, ribs (wall of thorax) ; *S*, sternum.

*visceral layer* may be distinguished (Fig. 240, B, C): the latter is spoken of as the *pulmonary pleura*, the former as the *costal pleura*.

Towards the middle line, the pulmonary pleura of either side is reflected so as to form a septum between the right and left thoracic cavities. This septum is called the *mediastinum*, and the space between its two layers the *mediastinal space:* through this, the aorta, œsophagus, and postcaval vein run, and in the region of the heart the mediastinum is reflected over the parietal layer of the pericardium.

There is a lymphatic fluid between the two layers of the pleura which renders the movements of the lungs smooth and easy.


## ABDOMINAL PORES.

By the term abdominal pore is understood a perforation—usually paired—of the posterior end of the wall of the peritoneal cavity which puts the cœlome into direct communication with the exterior.[1]

In Cyclostomes a pair of pores opens into the urinogenital sinus, serving to conduct the generative products to the exterior: they probably do not correspond to the abdominal pores of other forms, which never have this function, and are better described as *genital pores.*

In the Holocephali and Elasmobranchii the abdominal pores are usually paired and are situated posteriorly to the cloaca (Figs. 206, 289, 290), and may be enclosed within its lips. They are wanting in the Notidanidæ, Cestracionidæ, and Rhinidæ, and are not constantly present in the Scylliidæ, even in individuals of the same species. In Ganoids, they open between the urinogenital aperture and anus, but are apparently wanting in Amia. Amongst Teleosts, they are said to be present only in the Salmonidæ and Mormyridæ, right and left of the anus ; but even in these, the pore of one or of both sides may be absent. In the Murænidæ, there is a single *genital pore,* which is apparently more nearly comparable to the similarly named structure in other Teleosts (*see* under Generative Organs) and to the genital pores of Cyclostomes. In Ceratodus the abdominal pores are paired, and open behind the cloaca, while in Protopterus a single, apparently blind, canal is present on the same side of the ventral fin as the vent (Fig. 209), sometimes to the right and sometimes to the left of the middle line, either within or without the sphincter of the cloaca.

Abdominal pores are not known to occur in the Amphibia and Mammalia, but amongst Reptiles they are perhaps represented by the *peritoneal canals* of the Chelonia and Crocodilia, which in the former are in close relation with the penis or clitoris, and usually end blindly.

[1] The abdominal pores may possibly correspond to the remains of segmental ducts. Other connections of the cœlome with the exterior (by means of the nephrostomes of Anamnia and the ostia of the oviducts in the majority of Vertebrata) will be mentioned in a subsequent chapter.

## H.  ORGANS OF CIRCULATION.

## (VASCULAR SYSTEM.)

THE organs of circulation, which arise from the mesoblast,[1] consist, in the Craniata, of a hollow central muscular organ, the **heart**, which is connected with a series of completely closed tubes, the **blood-vessels**. The heart and blood-vessels contain a coloured fluid, the *blood*, and their cavities probably represent the remains of the blastocœle (p. 4). Another system of vessels containing a colourless fluid, the *lymph*, must be distinguished from the blood vessels: lymph, however, is present in various spaces or *sinuses* in the body as well as in the **lymph-vessels** (p. 333): the lymphatic system is, therefore, not completely closed, the vessels communicating with the sinuses on the one hand, and with the blood-vessels on the other.

Both blood and lymph consist of a colourless fluid, the *plasma*, in which float numerous *cells* or *corpuscles*. The *blood-corpuscles* are of two kinds—colourless, nucleated, amœboid cells, known as *white* or *colourless corpuscles* or *leucocytes*, and far more numerous *red blood-corpuscles* or *erythrocytes*.[2] The lymph contains colourless corpuscles only, and these are precisely similar to those of the blood. Both blood and lymph are kept in constant circulation through the vessels by the contraction of the heart, which acts both as a force-pump and a suction-pump, and they serve to carry the absorbed food and oxygen to, and the waste products from, all parts of the body.

All the blood vessels which bring back the blood to the heart are known as **veins**, while those which carry it from the heart are called **arteries**: the latter usually contain oxygenated, the former impure blood, but this is by no means always the case. Many of the veins are provided with *valves*, which are adapted to prevent the reflux of the blood: they have the form of semilunar folds of the internal coat, and each is usually made up of two folds,

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[1] According to some embryologists the hypoblast also takes part in the formation of the vascular system.

[2] In Amphioxus the blood contains white corpuscles only; there is no heart, and the vessels are only partially comparable to those of the Craniata.

placed opposite to one another.    The arteries (and also certain of
the veins) divide up into smaller and smaller branches, eventually
giving rise to microscopic tubes called **capillaries**, the walls
of which consist merely of a single layer of epithelial cells,
and these again unite to form the factors of the veins.    The walls
both of veins and arteries consist, in addition to the epithelium, of
connective and elastic tissue and of unstriated muscular fibres, and are
much thicker in the case of the arteries than in that of the veins,
in which the muscular elements may be altogether wanting.

The nucleus of the red corpuscles persist, and the whole cell is biconvex,
in all Vertebrates below Mammals ; and, even in these, nucleated red cells
may be seen in the marrow of the bones, in the blood of the spleen, and
often in that of the portal vein.    In all other parts of the body of Mammals
they lose their nuclei and become biconcave.    In all Mammals, except the
Camelidæ, the red corpuscles have the form of circular discs ; in the last-
mentioned group and in all other Vertebrates except Cyclostomes they are
oval.    They are largest in certain Urodeles, being in Amphiuma as much
as $75\mu$ in their longest diameter ; then come, in order, those of other
Urodeles and of Dipnoans, Reptiles, Anurans, Fishes, Birds, and Mammals,
in which latter order they are the smallest, varying in different families from
$2\cdot5\mu$ (Tragulidæ) to $10\mu$.

The heart is enclosed within a serous membrane, the *pericar-
dium* (Fig. 240c), which consists of parietal and visceral layers ;
the former is invested by the mediastinum (p. 298), and the latter
is closely applied to the heart.    Between the two layers is a space
filled with lymph, representing part of the cœlome ; this is usually
completely shut off from the abdominal cavity, but in Elasmo-
branchs the two communicate by means of pericardio-peritoneal
canals.

The heart arises either as a single (Elasmobranchii, Amphibia)
or as a paired (Teleostei, Sauropsida, Mammalia) tubular cavity
in the splanchnic layer of the mesoblast (comp. note on p. 299)
along the ventral region of the throat, close behind the gill-clefts.
Its wall becomes differentiated into three layers, an outer serous
(pericardial), a middle muscular, and an inner epithelial.    In this
respect it essentially corresponds with the larger vessels, in the walls
of which, as already mentioned, three layers can also be distinguished ;
but in the heart the muscular fibres are striated.    By a study of its
development we thus see that the heart corresponds essentially to
a strongly developed blood-vessel, which at first lies more or less in
the longitudinal axis of the body ; later, however, it becomes much
more complicated by the formation of various folds and swellings.
Thus the embryonic tubular heart becomes folded on itself and
divided into two chambers, an *atrium* or *auricle* and a *ventricle*
(Fig. 241).    Between these, valvular structures arise, which only
allow the blood to flow in a definite direction on the contraction of
the walls of the heart, viz., from the atrium to the ventricle ; any
backward flow is thus prevented.    The valves are formed by

a differentiation of the muscular trabeculæ of the walls of the heart. The atrium, into which the blood enters, represents primitively the venous portion of the heart; the ventricle, from which the blood flows out, corresponding to the arterial portion.

The venous end further becomes differentiated to form another chamber, the *sinus venosus*, and the arterial end gives rise distally to a *truncus arteriosus;* the proximal end of this (*conus arteriosus*) is provided with more or less numerous valves, and its distal end (*bulbus arteriosus*) is continued forwards into the arterial vessel (*ventral aorta*).

The *ventral aorta* gives off right and left a series of symmetrical *afferent branchial arteries* (Figs. 242, 243), each of which runs between two consecutive gill-clefts, branches out into capillaries in the gills, when present, and then becomes continuous with a corresponding *efferent branchial artery*. After the first pair of these has given off branches to the head (*carotids*), they all unite above the clefts to form a longitudinal trunk on either side, and there form the right and left roots of the *dorsal aorta ;* this extends backwards along the ventral side of the vertebral axis into the tail as a large unpaired trunk, which gives off



FIG. 241.—DIAGRAM SHOWING THE PRIMITIVE RELATIONS OF THE DIFFERENT CHAMBERS OF THE HEART.

*Sv*, sinus venosus, into which the veins from the body open ; *A*, atrium ; *V*, ventricle ; *Ca*, conus arteriosus ; *Ba*, bulbus arteriosus, from which the main artery arises.

numerous branches—including paired *vitelline* or *omphalo-mesenteric arteries* to the yolk-sac, and (except in Fishes and Dipnoans) *allantoic arteries* to the embryonic urinary bladder or allantois (pp. 9 and 337, and Figs. 8, 9, 242, 244).

Primarily, the blood becomes purified in the vessels which branch out over the yolk-sac, from whence it is returned by the *vitelline* or *omphalo-mesenteric* veins (Fig. 244). These join with the *allantoic veins* and veins of the alimentary canal to form what eventually becomes the *hepatic portal vein*, which divides up into capillaries in the liver. These capillaries then unite to form the *hepatic veins*, which open into the sinus venosus.

Into the sinus venosus there also opens on either side a *precaval vein* or *anterior vena cava*, which receives an *anterior cardinal* or *jugular vein* from the head, and a *posterior cardinal vein* from the body generally (not including the alimentary canal). The *caudal vein* which lies directly below the caudal aorta, is connected with the posterior cardinals, usually indirectly, through the *renal portal veins* (comp. Fig. 264). The further development of the embryonic vessels may take place in one of three ways.

The embryo may either leave the egg, and take on an aquatic

existence (Anamnia), making use of its branchial vessels for purposes of respiration, the entire allantois, in the case of the Am-
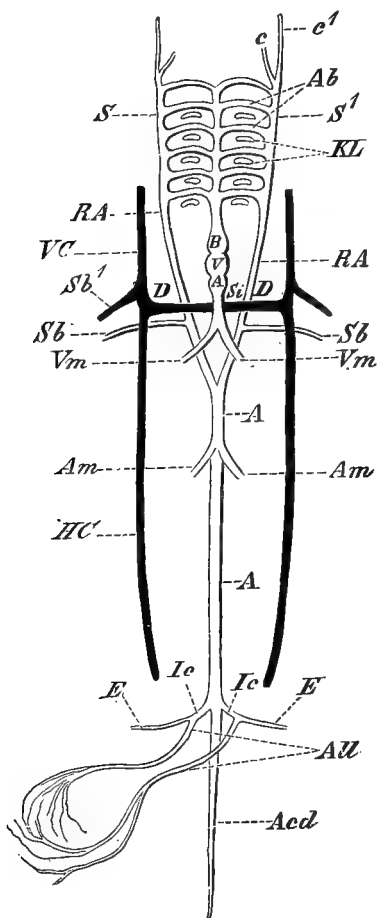
FIG. 242.—DIAGRAM OF THE EMBRYONIC VASCULAR SYSTEM.
(The portal systems are not shown.)

$A$, $A$, dorsal aorta; $RA$, $RA$, right and left roots of the aorta, which arise from the branchial vessels, $Ab$, by means of the collecting trunks, $S$, $S^1$; $c$, $c^1$, the carotids; $Sb$, subclavian artery; $KL$, gill-clefts; $Si$, sinus venosus; $A$, atrium; $V$, ventricle; $B$, truncus arteriosus; $Vm$, vitelline veins; $Am$, vitelline arteries; $Ic$, $Ic$, common iliac arteries; $E$, $E$, external iliac arteries; $All$, allantoic (hypogastric) arteries; $Acd$, caudal artery; $VC$, $HC$, anterior and posterior cardinal veins; $Sb^1$, subclavian vein; $D$, precaval veins (ductus Cuvierii), into which the anterior and posterior cardinals open.

phibia, giving rise to the bladder. In the Amniota, which from the first breathe by means of lungs, a modification and reduction of
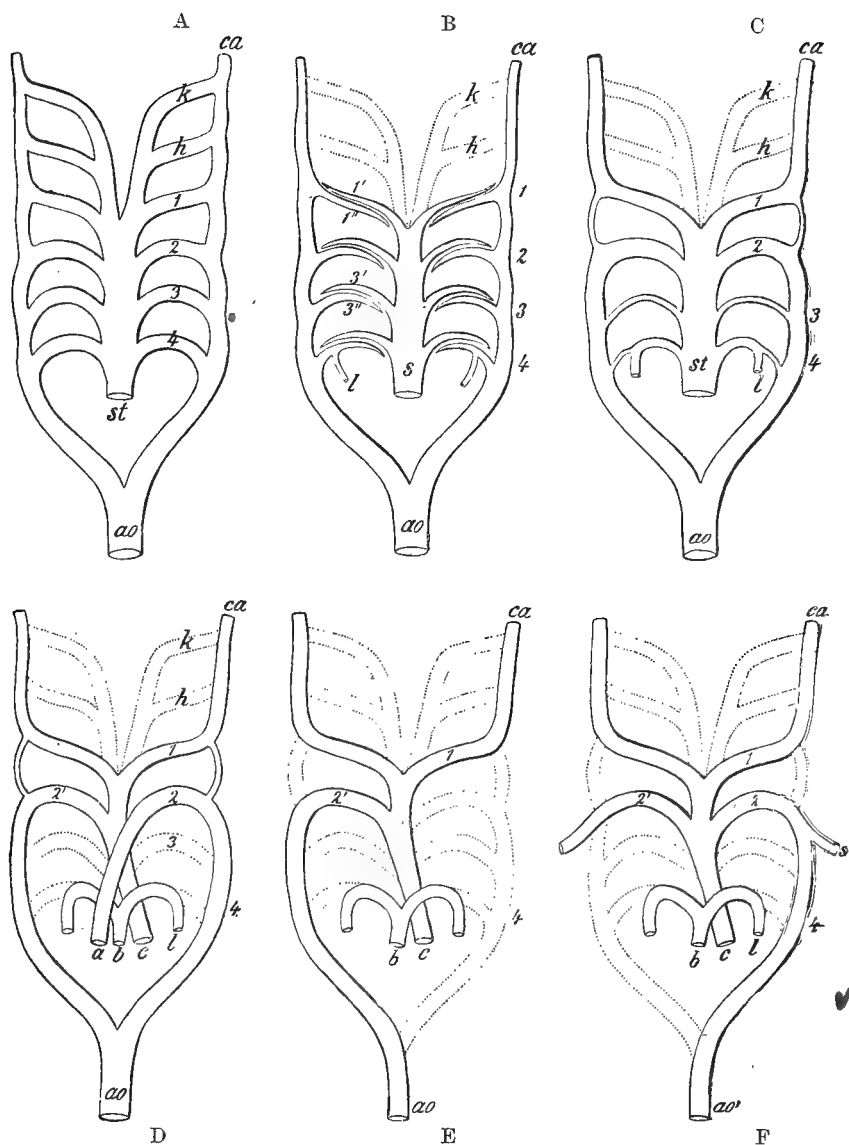
FIG. 243.—DIAGRAM OF THE ARTERIAL ARCHES OF VARIOUS VERTEBRATES.
(After Boas.)

A, embryonic condition; B, Fish; C, Urodele; D, Reptile (Lizard); E, Bird;
F, Mammal. The parts which disappear are dotted.

k and h, the two first embryonic arches, which almost always disappear; 1—4,
the four more posterior arches; $1^1$ and $3^1$, first and third afferent branchial
arteries; $1''$ and $3''$, the corresponding efferent branchial arteries; 2 in D and
F, second arch of the left side; $2^1$ in D, E and F, second arch of the right
side; a, b, c, the vessels into which the ventral arterial trunk is divided in
Reptiles, Birds, and Mammals; ao, dorsal aorta; ca, carotid; l, pulmonary
artery; s (in F), left subclavian artery; st, and s (in B), ventral aorta.

the branchial vessels and allantois takes place, and the latter may even disappear entirely (see under Urinary organs). In the third case, the embryo undergoes a longer intra-uterine existence, the allantois coming into close connection with the walls of the uterus by means of the chorionic villi : the allantoic vessels extend into the wall of the uterus and come into more or less close relations with
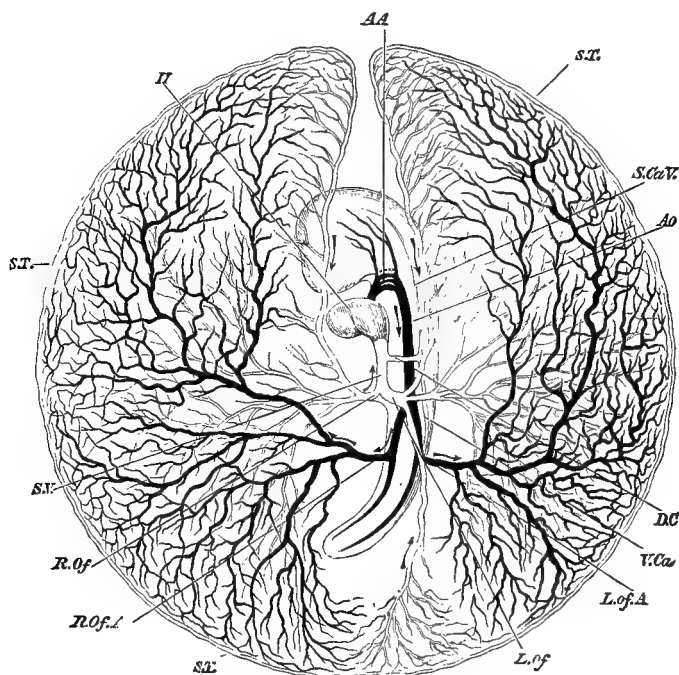


FIG. 244.—DIAGRAM OF THE CIRCULATION OF THE YOLK-SAC AT THE END OF THE THIRD DAY OF INCUBATION IN THE CHICK.   (After Balfour.)

*H*, heart ; *AA*, the second, third, and fourth aortic arches : the first has become obliterated in its median portion, but is continued at its proximal end as the external carotid, and at its distal end as the internal carotid ; *Ao*, dorsal aorta ; *L.Of.A*, left vitelline artery ; *R.Of.A*, right vitelline artery ; *S.T*, sinus terminalis ; *L.Of*, left vitelline vein ; *R.Of*, right vitelline vein ; *S.V*, sinus venosus ; *D.C*, ductus Cuvieri ; *S.Ca.V*, anterior cardinal or jugular vein ; *V.Ca*, posterior cardinal vein.   The veins are marked in outline, and the arteries are made black.   The whole blastoderm has been removed from the egg, and is supposed to be viewed from below.   Hence the left is seen on the right, and *vice versa*.

the maternal vessels, thus serving for the respiration and nutrition of the fœtus. In this way a placenta and a placental circulation arise (comp. Fig. 9, and pp. 9 and 337).

On the appearance of pulmonary respiration, important changes take place in the branchial vessels and heart. The formation of a septum in both the atrium and ventricle leads to the presence

of two atria or auricles, and two ventricles, and the conus arteriosus and sinus venosus become eventually more or less incorporated in the ventricles and right auricle respectively. Thus a right (venous) and a left (arterial) half can be distinguished ; and a new vessel, the *pulmonary artery*, arising from the last arterial arch, becomes connected with the right ventricle : this conveys venous blood to the lungs, while special vessels (*pulmonary veins*) return the oxygenated blood from the lungs to the left auricle, from which it passes into the left ventricle and so into the general circulation of the body.

The branchial vessels never become functional as such, in any period of development either in Sauropsida or Mammalia ; but those which persist give rise, as already mentioned, to important vascular trunks of the head, neck (carotids), anterior extremities (sub-clavians), and lungs (pulmonary arteries), and also to the roots of the aorta, one or both of which may remain (comp. Fig. 243).

The primitive number of arterial arches is six, the first two of which (belonging to the mandibular and hyoid arches respectively) almost always disappear early : in caducibranchiate Amphibia (including Anura) and in Amniota, the fifth arch also disappears. The third gives rise to the *carotid arch* ; the fourth of both sides (Amphibia, Reptilia), or of one side (Aves, Mammalia), to the *aortic* or *systemic arch*, and the sixth to the *pulmonary arch* (Fig. 243).

From the Dipnoi onwards, the posterior cardinals become more or less completely replaced functionally by a large unpaired vein, the *postcaval* or *posterior vena cava*, which opens independently into the right auricle.

## The Heart, together with the Origins of the Main Vessels.

**Fishes** (including **Cyclostomes**).—The heart in Fishes is situated in the anterior part of the body-cavity, close behind the head. It is formed on the same general plan as that described on p. 300, consisting of a ventricle with a truncus arteriosus or merely a bulbus (Cyclostomi, Teleostei), and an atrium or auricle, the latter receiving its blood from a sinus venosus, and being laterally expanded to form the *appendices auriculæ* (Figs. 245 and 246).

In correspondence with the work which each portion has to perform, the walls of the atrium are thin, while those of the ventricle are much stronger, its muscles giving rise in the interior to a network and usually to a series of large trabeculæ : this holds good through-out the Craniata.

Between the sinus venosus and atrium, and also between ventricle and atrium, membranous valves are present ; there are primarily two atrioventricular valves, but they may be further sub-divided. Numerous valves, arranged in rows, are present in the

muscular conus arteriosus (Fig. 246, A) : these are most numerous in Elasmobranchs and Ganoids. There is a tendency, however, for the posterior valves, or those which lie nearest the ventricle,
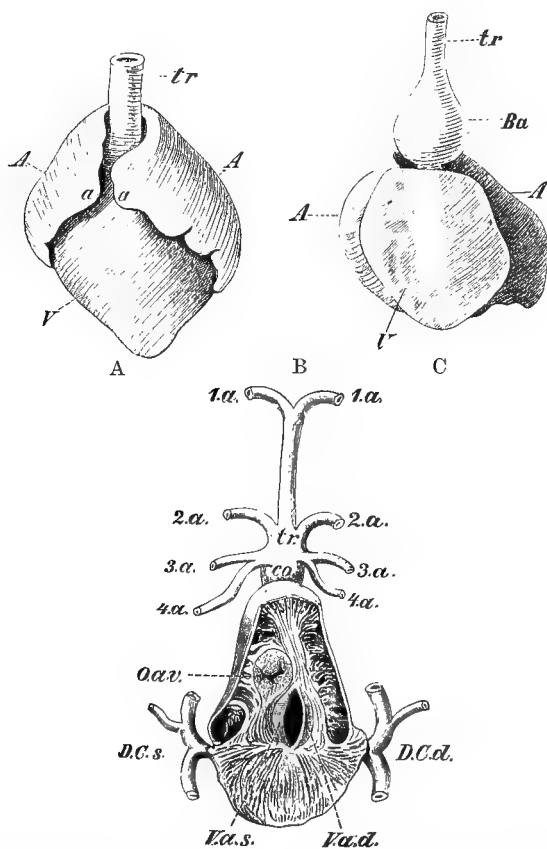


FIG. 245.—HEART OF A, *Zygœna malleus*, FROM THE VENTRAL SIDE ; B, OF *Acanthias vulgaris*, FROM THE DORSAL SIDE, WITH THE ATRIUM CUT OPEN (after Röse) ; C, OF A TELEOST (*Silurus glanis*).

*A, A*, atria ; *a, a*, auricular appendages ; *V*, ventricle ; *tr* (in B) and *Ba* (in C), bulbus arteriosus ; *tr* (in A) and *co* (in B), conus arteriosus, *tr* (in C), ventral aorta.

*D.C.d* and *D.C.s*, right and left precavals ; *V.a.d.* and *V.a.s*, right and left valve of the sinus venosus ; *O.a.v*, atrio-ventricular aperture ; 1,*a*—4,*a*, afferent branchial arteries.

gradually to undergo reduction (B). The most anterior row always persists, and corresponds to the single row of valves between the ventricle and bulbus in Teleosts (C) and Cyclostomes. Together with the reduction of these valves, the conus arteriosus also becomes reduced in the last-mentioned forms, so that the non-

contractile bulbus arteriosus usually lies close against the ventricle (Fig. 246, c).

The heart of Fishes contains venous blood only, which it forces
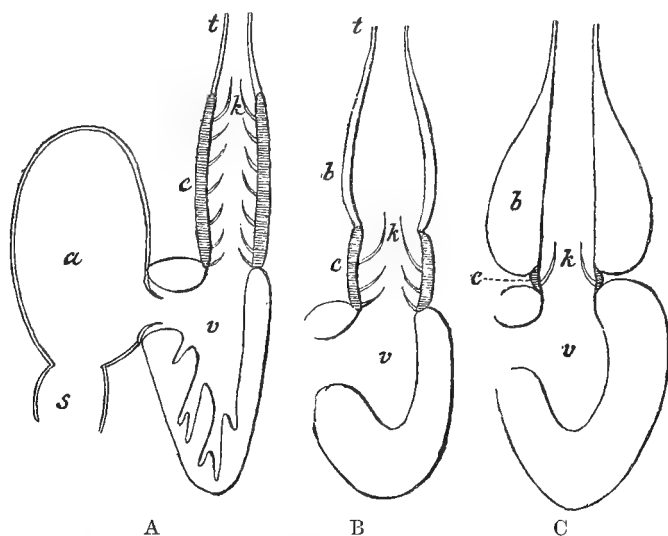


FIG. 246.—DIAGRAMMATIC LONGITUDINAL SECTION THROUGH THE HEARTS OF VARIOUS FISHES. (From Boas's *Zoology*.) *A*, Fish with well developed conus arteriosus (*e.g.*, Elasmobranch); *B*, Amia ; *C*, a Teleost. In *B* and *C* the sinus venosus and atrium are not indicated.

*a*, atrium ; *b*, bulbus arteriosus ; *c*, conus arteriosus ; *k*, valves ; *s*, sinus venosus ; *t*, ventral aorta ; *v*, ventricle.

through the afferent branchial arteries (Figs. 243, B, 245, C, and 264) into the capillaries of the gills, where it becomes oxygenated, to pass thence into the efferent branchial arteries, and so into the aortic roots.

**Dipnoi.**—In the Dipnoi, as in Fishes proper, the heart lies far forwards, near the head. In correspondence with the double mode of respiration, by lungs as well as by gills, it reaches a stage of development mid-way between that seen in Elasmobranchs and in Amphibians (Figs. 247 and 248). The atrium becomes divided into a *left* and a *right* chamber by a septum, as does also the ventricle to some extent, owing to the presence of a cushion composed of muscular fibres and connective-tissue (Fig. 247) situated between the atrium and ventricle, and extending into both of these chambers : this acts as a valve, ordinary atrio-ventricular valves being absent. The sinus venosus, from the Dipnoi onwards, opens into the right atrium.

The conus arteriosus is twisted spirally on itself (Fig. 248) : in Ceratodus it is provided with eight transverse rows of valves, and

x 2
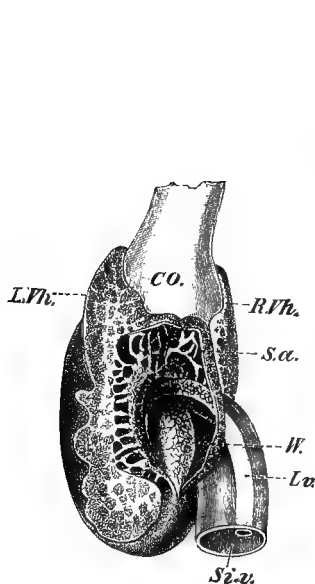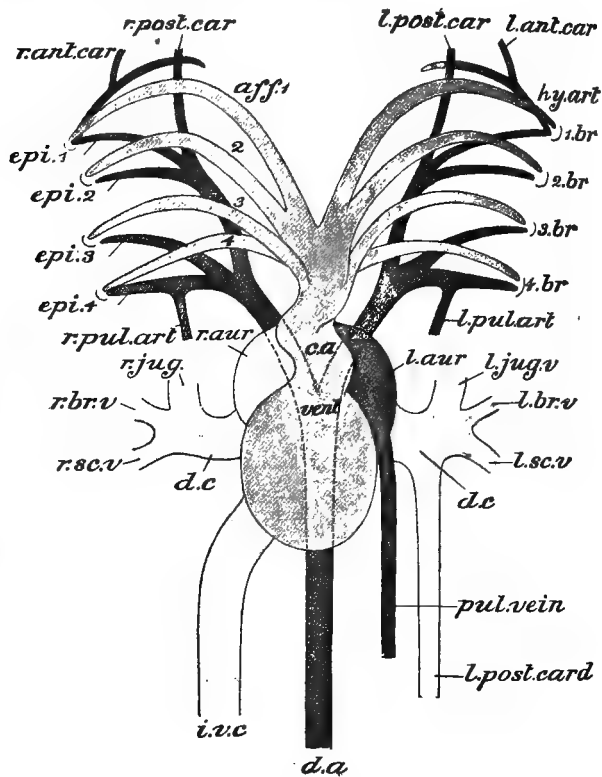
FIG. 247.

FIG. 248.

FIG. 247.—HEART OF *Protopterus annectens*. From the left side, part of the wall of the left atrium being removed. (After Röse.)

*W*, fibrous cushion extending into the ventricle; *Si.v*, sinus venosus, within which the pulmonary vein (*Lv*) extends to open into the left auricle by a valvular aperture; *L.Vh* and *R.Vh*, left and right atria; *S.a*, septum atriorum; *Co*, conus arteriosus.

FIG. 248.—*Ceratodus forsteri*. DIAGRAMMATIC VIEW OF THE HEART AND MAIN BLOOD VESSELS AS SEEN FROM THE VENTRAL SURFACE. (From Parker and Haswell's *Zoology*, after Baldwin Spencer.)

*aff.* 1, 2, 3, 4, afferent branchial arteries; 1 *br*, 2 *br*, 3 *br*, 4 *br*, position of gills; *c.a*, conus arteriosus; *d.a*, dorsal aorta; *d.c*, ductus Cuvieri; *epi.*1, *epi.*2, *epi.*3, *epi.*4, efferent branchial arteries; *hy.art*, hyoidean artery; *i. v. c*, postcaval vein; *l.ant.car*, left anterior carotid artery; *l.aur*, left auricle; *l.br.v*, left brachial vein; *l.jug.v*, left jugular vein; *l.post.car*, left posterior carotid artery; *l.post.card*, left posterior cardinal vein; *l.pul.art*, left pulmonary artery; *l.sc.v*, left sub-scapular vein; *r.ant.car*, right anterior carotid artery; *r.aur*, right auricle; *r.br.v*, right brachial vein; *r.jug.v*, right jugular vein; *r.post.car*, right posterior carotid; *r.pul.art*, right pulmonary artery; *r.sc.v*, right sub-scapular vein; *vent*, ventricle.

begins to be divided into two chambers. In Protopterus this division is complete, so that two currents of blood, mainly arterial and

mainly venous respectively, pass out from the heart side by side. The former comes from the pulmonary vein, from which it passes into the left atrium, thence into the left side of the ventricle, and so to the two anterior branchial arteries. The venous current, on the other hand, passes from the right side of the ventricle into the third and fourth afferent branchial arteries and thence to the corresponding gills, where it becomes purified; it reaches the aortic roots by means of the efferent branchial arteries. The paired *pulmonary artery* arises from the fourth efferent branchial in Ceratodus (Fig. 248), and from the aortic root in Protopterus and Lepidosiren, that of the right side bifurcating to supply the dorsal surface of the lung or lungs (p. 288), while that of the left side supplies the ventral surface. The two pulmonary veins unite to form a median trunk which becomes closely connected with the sinus venosus, so as to appear sunk within its walls (Fig. 247). Thus the blood becomes once more purified before it passes into the left ventricle. A *postcaval* vein, present from the Dipnoi onwards, opens into the sinus venosus posteriorly to the precavals, and with it the hepatic veins communicate (Figs. 248 and 267).

**Amphibia.**—With the exception of the Gymnophiona, in which it is situated some distance back, the heart in all Amphibians lies far forwards, below the anterior vertebræ. A septum atriorum is well developed, but in Urodela and Gymnophiona it is more or less fenes-
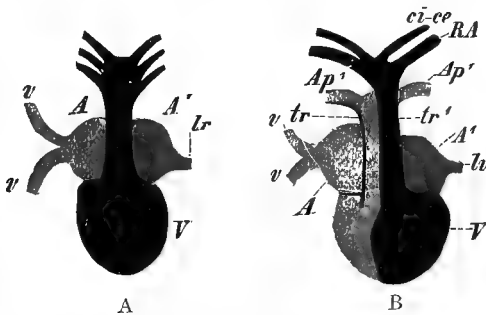


FIG. 249.—DIAGRAM SHOWING THE COURSE OF THE BLOOD THROUGH THE HEART IN *Urodela* (A) AND *Anura* (B).

A, right atrium; $A^1$, left atrium; $V$, ventricle; $tr$, conus arteriosus, divided in Anura (B) into two portions, $tr$, $tr^1$: through $tr$ venous blood passes into the pulmonary arteries, $Ap^1$, $Ap^l$, while through $tr^1$ mixed blood goes to the carotids, $ci$—$ce$, and to the roots of the aorta, $RA$; $lr$, $lr$, pulmonary veins; $r$, $r$, pre- and post-cavals (only one precaval is indicated).

trated (Fig. 250). There are always two fibrous, pocket-like atrioventricular valves, which are connected with the walls of the ventricle by cords. The two pulmonary veins unite before opening into the left atrium.

The cavity of the ventricle is unpaired, and neither in Urodela nor Anura shows any trace of a septum, so that the blood passing out from it must have a mixed character (Fig. 249). The ventricle is usually short and compressed, but is more elongated in Amphiuma, Proteus, and the Gymnophiona. It is continued anteriorly into a conus arteriosus, as in Elasmobranchs, Ganoids, and Dipnoans; this has usually a slight spiral twist, and possesses a transverse row of valves at either end, as well as a spiral fold extending into its lumen.[1] This holds good for the Axolotl, Amblystoma,
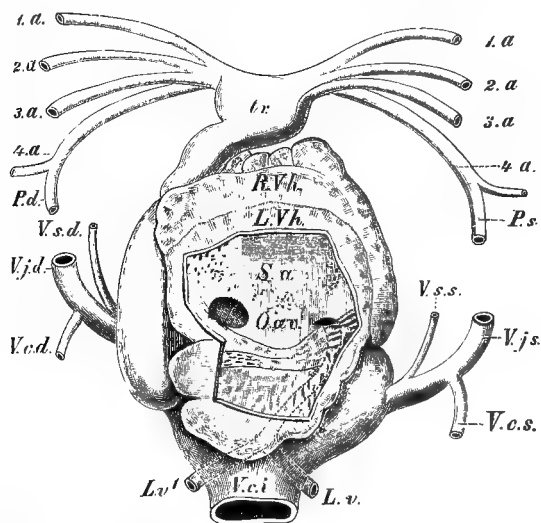


FIG. 250. HEART OF *Cryptobranchus japonicus.* From the ventral side. (After Röse.) The left atrium is cut open.

*S.a*, septum atriorum, perforated by numerous small apertures; *L.v*, *L.v*[1], the two pulmonary veins, opening by a single aperture into the left atrium; *O.ar*, atrio-ventricular aperture; *1*[a], *4*[a], the four arterial arches; *P.d.* and *P.s*, left and right pulmonary arteries; *tr*, truncus arteriosus; *L.Vh*, *R.Vh*, left and right atria; *V.s.d* and *V.s.s*, subclavian veins; *V.j.d* and *V.j.s*, jugular veins; *V.c.d*, *V.c.s*, posterior cardinal veins; *V.c.i*, postcaval vein.

Salamandra, Amphiuma, and Siren. In others (*e.g.*, Necturus, Proteus, Gymnophiona), retrogression is seen in a lengthening of the conus, the disappearance of the spiral fold, and the presence of only a single row of valves.

In Anura, the fold lying within the conus extends so far back that no undivided portion of the cavity is left. The consequence of this is that the blood passing into the hindermost pair of the arterial arches—that from which the pulmonary arteries arise—is mainly venous, while the others contain more or less mixed blood (Fig. 249, B) ; for, owing to the spongy nature of the ventricle, there

[1] This spiral fold corresponds to a series of fused valves.

is no time for its contained blood to get thoroughly mixed before it is forced into the conus.

As in the Dipnoi, four afferent branchial arteries (Fig. 250) arise on either side from the short conus in the Amphibia, which —taking as a type the larva of Salamandra—have the following relations (comp. Fig. 243, c).

The three anterior arteries pass to numerous external gill-tufts, in which they break up into capillaries (Fig. 251). From the latter three efferent vessels arise, which pass to the dorsal side, and there unite on either side to form the aortic root. The fourth afferent
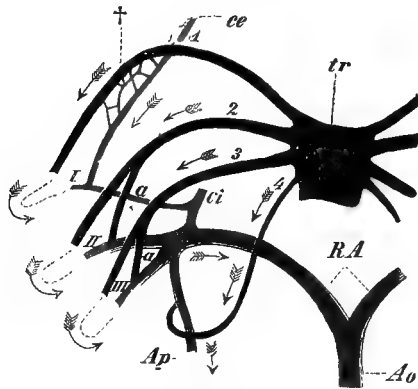


FIG. 251.—THE ARTERIAL ARCHES OF THE LARVA OF A SALAMANDER. (Slightly diagrammatic.) (After J. E. V. Boas.)

*tr*, truncus arteriosus ; 1 to 3, the three afferent branchial arteries ; *I* to *III*, the corresponding efferent arteries ; 4, the fourth arterial arch, which becomes connected with the pulmonary artery $(Ap)$ ; $a$, $\omega$, direct anastomoses between the second and third afferent and efferent branchial arteries ; *ce*, external carotid ; *ci*, internal carotid ; †, net-like anastomoses between the external carotid and the first afferent branchial artery, which give rise later to the "carotid gland" ; *RA*, aortic roots ; *Ao*, dorsal aorta. The arrows show the course which the blood takes.

branchial artery, which is smaller than the others, does not pass to a gill, but to the pulmonary artery, which arises from the third efferent branchial. The pulmonary artery, therefore, contains far more arterial than venous blood, and thus the lungs of the Salamander larva, like the air-bladder of Fishes, can only be of secondary importance in respiration.

The *internal carotid* arises from the first afferent branchial artery, towards the middle line, the *external carotid* coming off further outwards (Fig. 251). The latter, as it passes forwards, becomes connected with the first afferent branchial by net-like anastomoses, and these give rise later to the so-called "*carotid gland*"[1]

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[1] The "carotid gland" loses its character as a *rete mirabile* (comp. p. 333), and in the adult consists simply of a muscular vesicle with septa in its interior.

of the adult, which probably functions as an accessory heart. Direct connections exist between the second and third afferent and efferent arteries.

Towards the end of the larval period, the second efferent branchial artery increases considerably in relative size, and the fourth arterial arch also becomes larger. By a reduction of the anastomosis with the third arch, the fourth carries most of the blood for the pulmonary artery, and the latter thus now contains more venous than arterial blood. When branchial respiration ceases, the anastomoses between the afferent and efferent branchial arteries no longer consist of capillaries, but a direct connection between them becomes established (Fig. 252). Finally, the connection between the
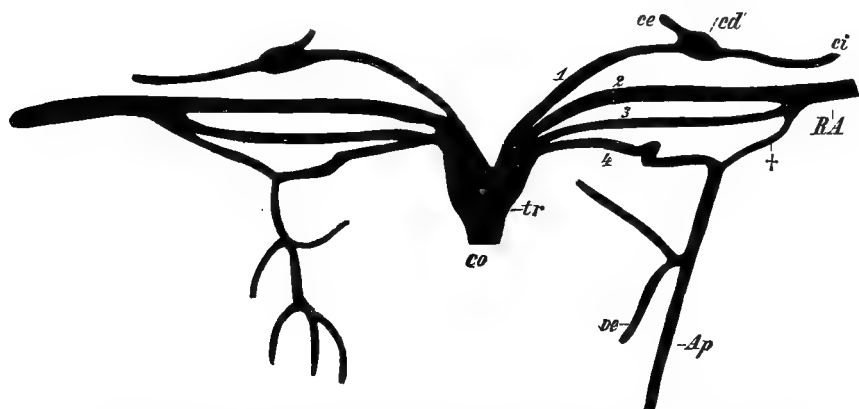


FIG. 252. —ARTERIAL ARCHES OF AN ADULT *Salamandra maculosa*, SHOWN SPREAD OUT. (After J. E. V. Boas.)

*co, tr,* truncus arteriosus ; 1 to 4, the four arterial arches ; *ce,* external carotid ; *cd,* " carotid gland " ; *ci,* internal carotid. The fourth arterial arch, which gives rise to the pulmonary artery (*Ap*), has increased considerably in size relatively, and is only connected by a delicate ductus Botalli (†) with the second and third arches ; *RA,* root of the aorta ; *œ,* œsophageal vessels.

first and second branchial arches disappears, the former giving rise to the carotid and the latter forming the large aortic root; an anastomosis remains throughout life, however, between the fourth arch, which forms the pulmonary artery, and the second and third arches. This is usually spoken of as the *ductus Botalli.*

The third arch varies greatly in its development; it may be present on one side only, or may even be entirely wanting.

In the larvæ of Anura there are also four afferent branchial arteries present on either side, but these are connected with the corresponding efferent vessels by capillaries only, there being no direct anastomoses (compare Fig. 251). The consequence of this is that *all* the blood becomes oxygenated.

In the adult Frog the third arterial arch becomes entirely

obliterated, and there is no ductus Botalli : the other vessels resemble those of the Salamander. In lungless forms (p. 290) a correlative reduction of the pulmonary vessels occurs.

**Reptiles.**—As in all Amniota, the heart of Reptiles arises far forwards in the neighbourhood of the gill-clefts, but on the formation of a neck it comes to lie much further back than is the case in
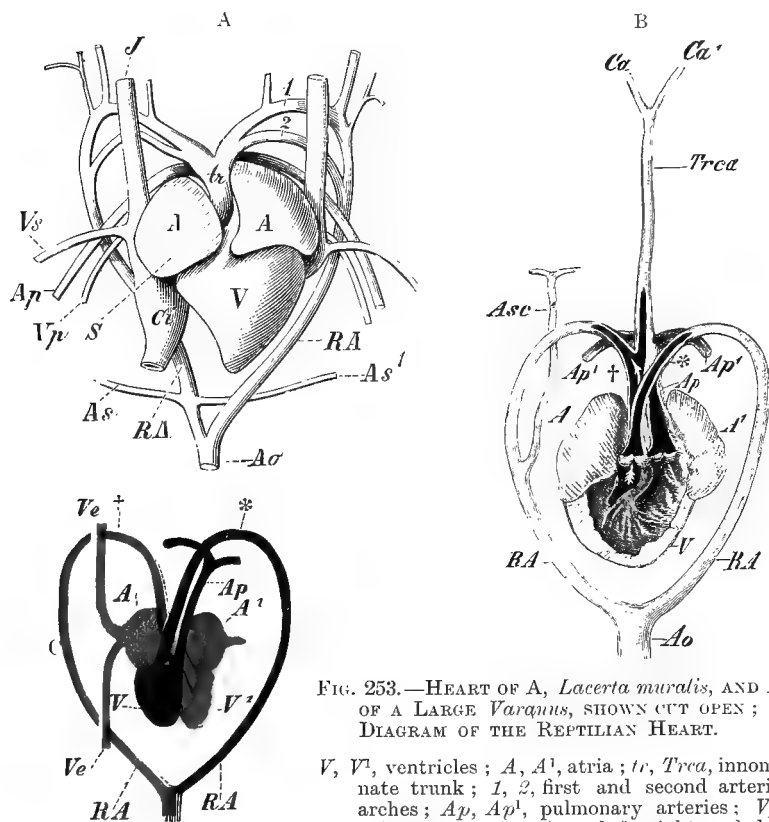


FIG. 253.—HEART OF A, *Lacerta muralis*, AND B, OF A LARGE *Varanus*, SHOWN CUT OPEN ; C, DIAGRAM OF THE REPTILIAN HEART.

$V$, $V^1$, ventricles ; $A$, $A^1$, atria ; $tr$, $Trca$, innominate trunk ; $1$, $2$, first and second arterial arches ; $Ap$, $Ap^1$, pulmonary arteries ; $Vp$, pulmonary vein ; † and *, right and left aortic arches ; $RA$, root of aorta ; $Ao$, dorsal aorta ; $Ca$, $Ca^1$, carotids ; $Asc$, $As$, subclavian arteries. $J$, jugular vein ; $Vs$, subclavian vein ; $Ci$, postcaval : these three veins open into the sinus venosus, which lies on the dorsal side of the heart, above the point indicated by the letter $S$. In the diagram C the pre- and postcavals are indicated by $Ve$, $Ve$, only one precaval being represented.

the Anamnia.[1] The carotid arteries and jugular veins are thus correspondingly elongated.

The principal advance in structure as compared with the Amphibian heart is seen in the appearance of a muscular *ventricular*

[1] It is situated furthest forwards in the majority of Lizards and in Chelonians : in Amphisbænians, Snakes and Crocodiles it lies much further back.

*septum,* which may be incomplete, as in Lizards (Fig. 253, B), Snakes, and Chelonians, or complete, as in Crocodiles.

The conus arteriosus now becomes practically absorbed into the ventricular portion of the heart, and each aortic root may be made up at its origin of *two* arches, anastomosing with one another (Lacerta, Fig. 243, A), or of *one* only (certain Lizards, Snakes, Chelonians, and Crocodiles, Figs. 253, B, 255), from which the carotid artery arises directly. The left and right aortic arches cross at their base, so that the left arises on the right side, and *vice versa.*[1] The most posterior arterial arch gives rise to the pulmonary artery (comp. Fig. 243, D).

The blood from the right ventricle passes into the pulmonary artery as well as into the left aortic arch, and, according as the septum
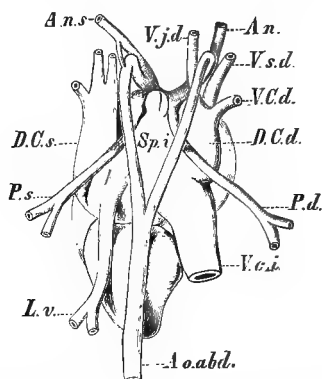


FIG. 254. —HEART OF *Cyclodus boddaertei.* From the dorsal side. (After Röse). The sinus venosus is almost entirely absorbed into the right atrium.

*D.C.s, D.C.d,* precaval veins ; *V.c.i,* postcaval vein ; *V.j.d,* jugular, *V.s.d,* sub-clavian, and *V.C.d.* posterior cardinal vein of the right side. *L.v,* pulmonary vein ; *P.s, P.d,* pulmonary arteries ; *An.s, An,* innominate arteries ; *Ao.abd,* dorsal aorta ; *Sp.i,* spatium intersepto-valvulare (comp. Fig. 257).

ventriculorum is complete or incomplete, is either entirely venous (Crocodiles) or mixed (other Reptiles, Fig. 253, C).

The valves of the heart have undergone a considerable reduction in Reptiles : at the origin both of the aorta and of the pulmonary artery there is only a single row ; this is also the case in all other Amniota. In Crocodiles the right atrio-ventricular aperture is guarded by a large muscular valve on the right (outer) side of the aperture.

The sinus venosus, which even in the Amphibia—especially Anura—shows indications of becoming sunk into the right atrium, is now usually no longer recognisable as a distinct chamber ex-

[1] A small aperture of communication between the two aortic roots, the *foramen Panizzæ,* exists in Crocodiles.

ternally (Figs. 254—256). It becomes partially divided into two portions by a septum ; and the left precaval, opening on the left of
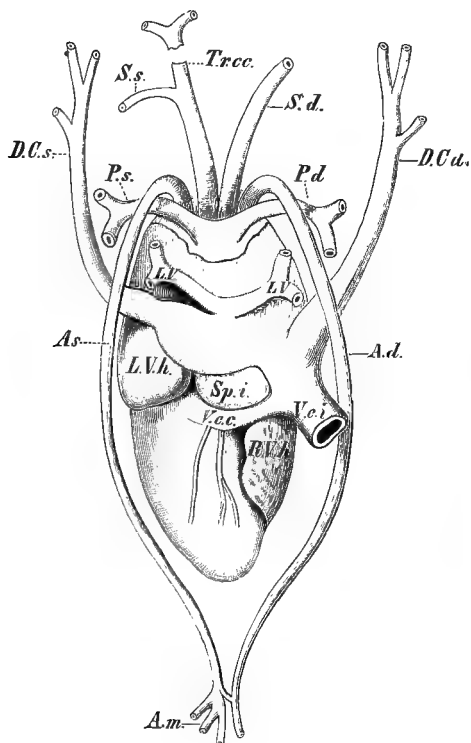


FIG. 255. FIG. 256.

FIG. 255.—HEART OF A YOUNG *Crocodilus niloticus.* From the dorsal side. (After Röse).

*Tr.cc*, common carotid ; *S.s, S.d*, subclavian arteries ; *A.s* and *A.d*, left and right aortic arches ; *A.m*, mesenteric artery ; *L.V.h, R.V.h*, left and right atria ; *V.c.c*, coronary vein. Other letters as in Fig. 244.
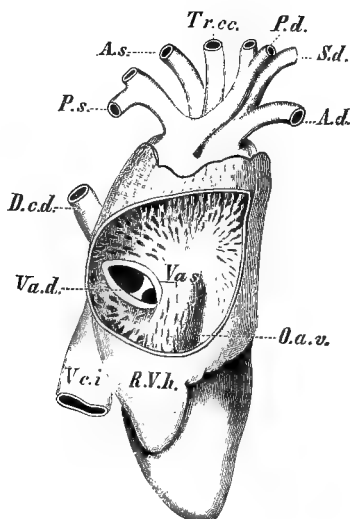
FIG. 256.—HEART OF *Crocodilus niloticus.* From the right side. (After Röse). Part of the wall of the right atrium is removed.

*O.a.v*, atrio-ventricular aperture ; *Va.d* and *Va.s*, the two sinu-auricular valves, the white line between which is the margin of the sinu-atrial septum. Other letters as in Figs. 244 and 245.

this septum, may appear to enter the right atrium independently (*e.g.*, Snakes.) The pulmonary veins unite into a single trunk before entering the left atrium.

**Birds and Mammals.**—In these Classes, the atrial and ventricular septa are always complete, and there is no longer any mixture

of the arterial and venous blood.  The muscular walls of the ventricle are strongly developed and very compact.   This is particularly the case in the left ventricle, on the inner wall of which the *papillary muscles* are well developed : the left ventricle is partially surrounded by the right, the cavity of the latter having a semilunar transverse section, and its walls being much thinner than those of the former (Fig. 258).

In both Birds and Mammals the blood from the head and body passes by means of the precavals and postcaval into the right
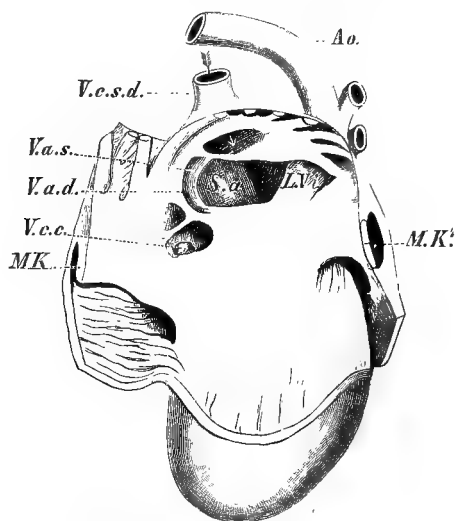


FIG. 257.—HEART OF GOOSE (*Anser vulgaris*), DISSECTED FROM THE RIGHT SIDE.
(After Röse.)

The right atrium and ventricle are cut open, and their walls reflected.  *S.a*, septum atriorum ;  *L. Vi*, limbus Vienssenii —a ridge arising from the ventral wall of the right atrium ;  the space between this and the septum atriorum is known as the spatium intersepto-valvulare (comp. Figs. 254 and 255).   *V.a.s*, *V.a.d*, the two sinu-auricular valves, situated at the entrance of the postcaval ; *MK*, *MK'*, muscular right atrio-ventricular valve ;  *Ao*, aorta ;  *V.c.s.d*, right precaval ;  *V.c.c*, aperture of coronary vein.

atrium, as does also that from the walls of the heart through the *coronary vein* [1] (Figs. 257, 259, 260, B), and the sinus venosus— especially in Mammals—is scarcely recognisable (Figs. 257, 260) : the right atrium is separated from the right ventricle by means of a well-developed valve.   In Birds (Fig. 257) this valve resembles that of Crocodiles, and is very large and entirely muscular, while in most Mammals it consists of three membranous lappets (tricuspid

[1] *Coronary veins* are present in most of the lower Vertebrates also (comp. *e.g.*, Fig. 255), and the heart is supplied with arterial blood by *coronary arteries*, usually arising in Fishes from a hypobranchial artery connected with the efferent branchials or subclavians, and in higher forms from the base of the aorta.

valve) to which are attached tendinous cords,[1] arising from the
papillary muscles.

In Birds the left atrio-ventricular aperture is provided with a
valve consisting of three membranous folds : in Mammals there are
only two folds, and the valve is therefore known as the *bicuspid* or
*mitral ;* three semilunar pocket-like valves are also present at the
origins of the pulmonary artery and aorta in both Birds and
Mammals.

As regards the origin of the great vessels, Birds are distinguished
from Mammals by the fact that in them the *right,* while in Mammals
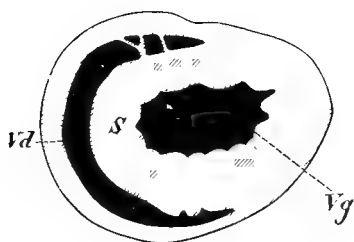


FIG. 258.



FIG. 259.

FIG. 258. —TRANSVERSE SECTION THROUGH THE VENTRICLES OF *Grus cinerea.*

*Vd,* right, and *Vg,* left ventricle ; *S,* septum ventriculorum.
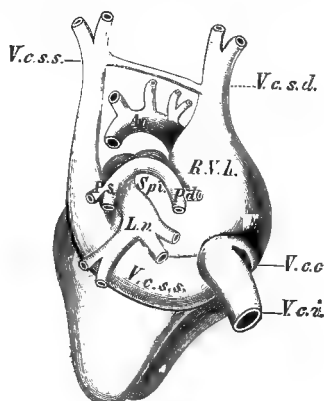
FIG. 259.—HEART OF *Ornithorhynchus paradoxus.* From the dorsal side.
(After Röse.)

*V.c.s.s, V.c.s.d,* precaval veins ; *V.c.i,* postcaval ; *V.c.c,* coronary vein ; *V.c.s.s,*
coronary sinus ; *L.v,* pulmonary veins ; *Ao,* aorta ; *P.s, P.d,* pulmonary
arteries ; *R.V.L,* right atrium ; *S.p.i,* Spatium intersepto-valvulare.

the *left* aortic arch persists (Fig. 243, E, F) ; the corresponding arch
of the other side in both cases gives rise to part of the subclavian
artery. Thus in both Birds and Mammals there is only *a single
aortic arch.* As in Amphibians, the posterior arterial arch gives
rise to the pulmonary artery. The pulmonary veins, two from
each lung, open close together into the left atrium (Fig. 259).

Amongst the more important points in the development of the
heart may be mentioned the fact that in the embryo the two atria
communicate with one another secondarily by means of the *foramen
ovale,* through which the blood from the postcaval passes into the
left ventricle (Fig. 260). This foramen closes up when the lungs

[1] There are no chordæ tendineæ in Monotremes, the heart of which in many
respects resembles that of the Sauropsida.

come into use, but its position can still be recognised as a thin area (*fossa ovalis*) in the atrial septum, surrounded by a fold (*annulus ovalis*). Extending from this to the base of the postcaval and right precaval respectively are two folds, known as the Eustachian and
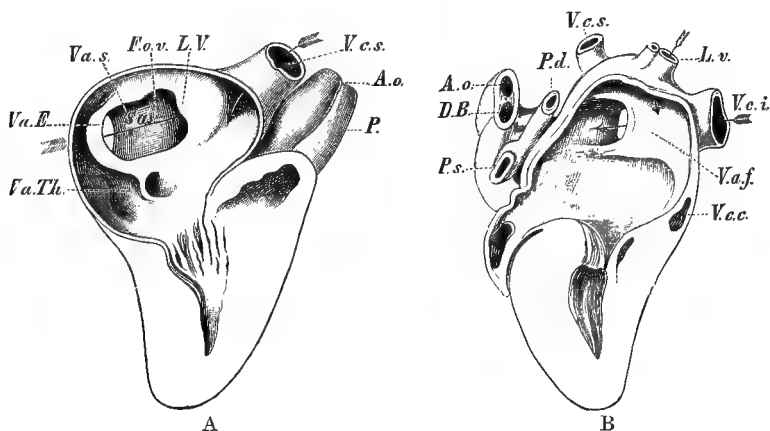


FIG. 260.—HEART OF HUMAN FŒTUS (8TH MONTH). A, From the right, and B, from the left side. (After Röse.) The walls of the atrium and ventricle are partly removed in each figure.

*Va.s*, left sinu-auricular valve, fused with the septum atriorum (*S.a, V.a.f*); *Va.Th*, Thebesian valve, in direct connection with the Eustachian valve (*Va.E*); *L.V*, left atrium; *F.o.v*, foramen ovale; *V.c.s*, left precaval; *V.c.i*, postcaval; *A.o*, aorta; *P, P.d, P.s*, pulmonary artery; *DB*, ductus Botalli (ductus arteriosus); *L.v.* pulmonary vein; *V.c.c*, coronary vein.

Thebesian valves (Fig. 260, A); these represent the remains of the right sinu-auricular valve, and serve in the embryo to conduct the blood from the right atrium into the left.

Great variations are seen in the mode of origin of the carotids and subclavians from the arch of the aorta in Mammals. Thus
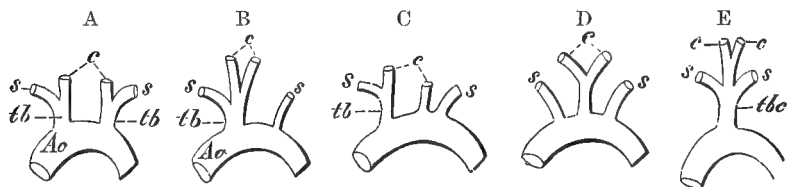


FIG. 261.—FIVE DIFFERENT MODES OF ORIGIN OF THE GREAT VESSELS FROM THE ARCH OF THE AORTA IN MAMMALS.

*Ao*, aortic arch; *tb, tbc*, brachiocephalic trunk; *c*, carotids; *s*, subclavians.

there may be a *brachiocephalic* or *innominate trunk* on either side (Fig. 261, A); or an unpaired common brachiocephalic, from which the carotid and subclavian of one or both sides arise (B, C, E); or,

finally, a common trunk of origin for the carotids, the subclavians arising independently on either side of it (D).

## ARTERIAL SYSTEM.

The essential relations of the carotid arteries, dorsal aorta, and pulmonary arteries, as well as the embryonic vitelline arteries, have already been dealt with (pp. 301–305, Figs. 242, 264, &c.). An *external carotid* and an *internal carotid* arise on either side independently from the anterior efferent branchial arteries in Fishes and Dipnoans, but from the Amphibia onwards these vessels are formed by the bifurcation of each *common carotid*. In these higher types, the internal carotid passes entirely into the cranial cavity, and supplies the brain with blood, while the external carotid goes to the external parts of the head (face, tongue, and muscles of mastication).

The origin of the subclavian artery, which supplies the anterior extremity, is very inconstant, being sometimes symmetrical, sometimes asymmetrical. It arises either in connection with the posterior efferent branchial vessels, or from the roots or main trunk of the aorta (Figs. 262–264, &c.). Extending outwards towards the free extremity, the subclavian passes into the *brachial artery*, from which a dorsal and a ventral branch arise, and these subdivide again in the limb.

From the dorsal aorta, in which a thoracic and an abdominal portion can be distinguished in Mammals in addition to the caudal portion, arise *parietal* (*intercostal, lumbar*), and *cœliac, mesenteric,* and *urinogenital* arteries, supplying the body-walls and viscera respectively. These all vary greatly both in number and relative size ; thus, for instance, there is sometimes a single *cœliaco-mesenteric* artery (Fig. 262), sometimes a separate cœliac, and one or more mesenteric arteries (Fig. 264);[1] the *renal* and *genital arteries* also vary in number and arrangement. All the branches of the dorsal aorta, however, present primarily an approximately metameric character, their number becoming more or less reduced owing to a concentration of the vessels, which is more marked in short-bodied than in long-bodied Vertebrates.

The aorta is continued posteriorly into the *caudal artery,* which usually lies within a cœlomic canal enclosed by the ventral arches of the vertebræ (Figs. 262–264) ; the degree of its development is naturally in correspondence with the size of the tail. In cases where the latter is rudimentary, as in Anthropoids and Man for instance, the caudal aorta is spoken of as the *median sacral artery,* and the aorta here appears to be directly continued, not by it, but

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[1] The *cœliac* typically supplies the stomach, liver, and spleen ; one or more *anterior mesenterics* the whole intestine with the exception of the rectum, as well as the pancreas ; and a *posterior mesenteric* the rectum.
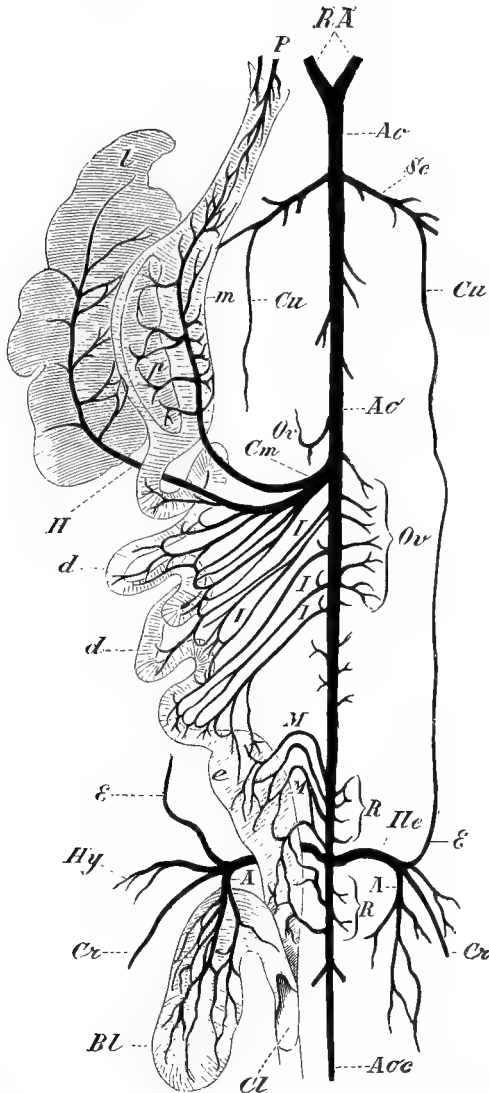
FIG. 262.—THE ARTERIAL SYSTEM OF *Salamandra maculosa*.

*RA*, roots of the aorta ; *Ao, Ao*, dorsal aorta ; *Sc*, subclavian artery, from which the cutaneous artery (*Cu*) arises : the latter anastomoses posteriorly with the epigastric artery *E* ; *Ov*, ovarian arteries ; *Cm*, cœliaco-mesenteric ; *H*, hepatic artery ; *I, I, I*, anterior mesenteric arteries passing to the small intestine ; *M, M*, posterior mesenteric arteries ; *R, R*, renal arteries ; *Ilc*, common iliac ; *Cr*, crural artery ; *Hy*, hypogastric artery ; *A, A*, vesical (allantoic) arteries ; *Aoc*, caudal aorta ; *P*, pharynx and œsophagus ; *m*, stomach ; *p*, pancreas ; *l*, liver ; *d, d*, small intestine ; *e*, rectum ; *Bl*, urinary bladder ; *Cl*, cloaca.
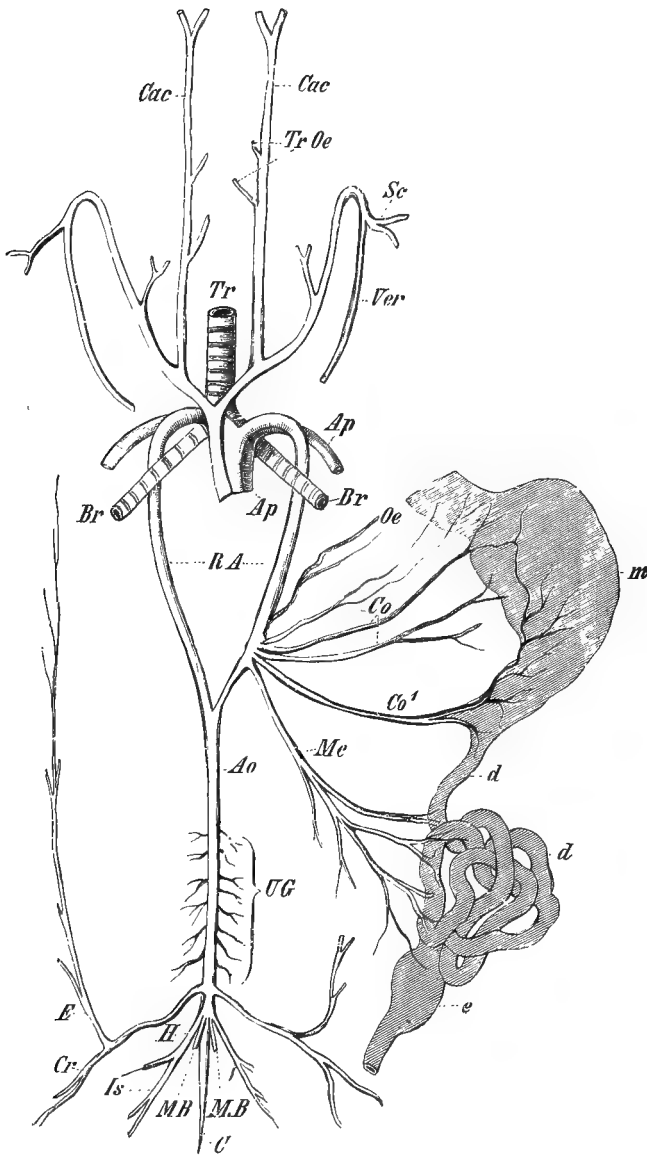
FIG. 263.—THE ARTERIAL SYSTEM OF *Emys europæa*.

*Tr*, trachea ; *Br, Br,* the two bronchi ; *m,* stomach ; *d, d,* small intestine ; *e,* large intestine ; *Ap,* pulmonary artery ; *Cac,* common carotids, with tracheal and œsophageal branches (*Tr, Oe*); *Sc,* subclavian artery; *Ver,* vertebral artery ; *RA,* roots of the aorta ; *Ao,* dorsal aorta ; *Co, Co¹,* and *Me,* cœliaco-mesenteric artery, which here arises as a bundle of separate vessels ; *UG,* urinogenital arteries ; *Cr,* crural artery ; *E,* epigastric artery ; *Is,* sciatic artery ; *MB,* posterior mesenteric arteries ; *C,* caudal aorta.

by the *common iliac arteries*, which pass outwards into the pelvic region.

Each common iliac artery becomes divided into an *internal iliac*, or *hypogastric*, supplying the viscera of the pelvis, and derived from the proximal portion of the embryonic allantoic artery, and an *external iliac*, which is continued into the *crural* or *femoral* and supplies the hinder extremity (Fig. 262). In some cases the internal and external iliacs come off separately from the aorta (Fig. 263). The function of the femoral may be largely taken by a *sciatic artery* arising separately from the aorta (Birds). The main vessels again branch out in the limb.

### Venous System.

**Fishes.**—Taking the Elasmobranchii more particularly into consideration, a few of the more important facts as regards the development of the veins must first be considered (comp. p. 301).

The first veins to appear in the embryo are the paired *omphalo-mesenteric veins*, which bring back the blood from the surface of the yolk and from the walls of the gut (Fig. 265, I, II). The vessels from the former region are known as *vitelline veins*, while those from the latter give rise to *subintestinal veins* (III—VII), running beneath the embryonic intestine, which primarily extends into the caudal region as the post-anal gut. On the disappearance of the latter, the posterior part of the subintestinal vessels gives rise to the *caudal vein*, which now lies directly beneath the caudal aorta and loses its direct connection with the anterior part (VIII—XII). As the liver is gradually developed, the main trunk of the left omphalo-mesenteric vein breaks up into capillaries within this organ, and these again unite anteriorly, opening into the proximal ends of both omphalo-mesenteric veins. The latter thus give rise to the *hepatic veins*, which open into the sinus venosus (or precaval, *e.g.*, in Cyclostomes). New vessels from the various parts of the alimentary canal (gastric, splenic, and mesenteric veins) are gradually developed, the pre-caudal portion of the subintestinal vein becoming of minor importance ; all these vessels unite to form what is now known as the *hepatic portal vein,* and thus pour their blood through the capillaries of the liver (Figs. 270, 264—268).

Anteriorly to the heart, a paired *precaval vein* (ductus Cuvieri) is developed (Figs. 264—268), and opens into the sinus venosus. This is formed, on either side, by the confluence of an *anterior* and a *posterior cardinal vein*, the former bringing back the blood from the head (*external* and *internal jugular* veins),[1] and the latter from the body,

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[1] A single or paired *inferior jugular* from the ventral part of the head may also be present (Fig. 266).
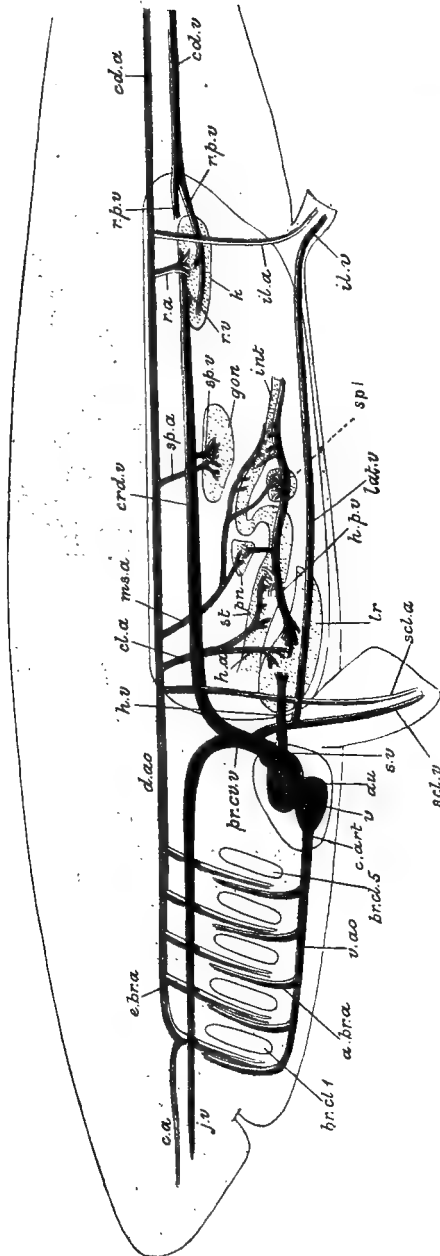
Fig. 264.—Semidiagrammatic Side View of the Vascular System of a Dogfish. (From T. J. Parker's *Elementary Biology*.)

s.v, sinus venosus ; au, atrium ; v, ventricle ; t.art, truncus arteriosus ; v.ao, ventral aorta ; a.br.a, afferent branchial arteries ; e.br.a, efferent branchial arteries ; d.ao, dorsal aorta ; c.a, carotid ; scl.a, subclavian artery ; cl.a, cœliac artery, supplying the stomach (st) and liver (lr) ; ms.a, mesenteric artery, supplying the intestine (int), pancreas (pn), and spleen (spl) ; sp.a, spermatic arteries ; r.a, renal arteries ; il.a, iliac artery ; cd.a, caudal artery.

j.v, jugular (anterior cardinal) vein ; cd.v, caudal vein ; r.p.v, renal portal ; r.v, revehent renal veins ; crd.v, posterior cardinal ; sp.v, spermatic veins ; pr.cv.v, precaval.

h.p.v, hepatic portal vein ; h.v, hepatic veins ; s.cl.v, subclavian vein ; il.v, iliac vein ; lat.v, lateral vein.

in which it runs on either side of the aorta, between it and the kidneys.   A *subclavian vein* from the pectoral fin also opens into
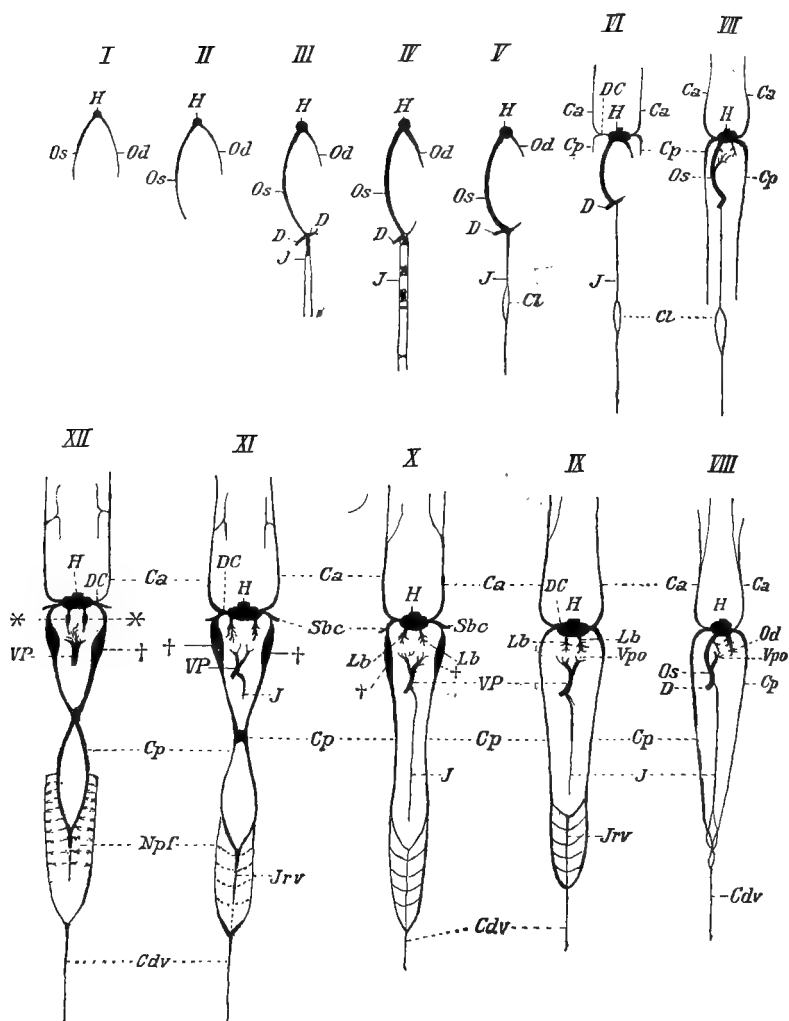
FIG. 265.—DIAGRAM OF STAGES IN THE DEVELOPMENT OF THE VEINS IN ELASMO-
BRANCHS. (I—XI after Rabl, XII after F. Hochstetter.)

*Ca, Cp,* anterior and posterior cardinal veins ; *Cdv,* caudal vein ; *D,D,* vitelline
veins ; *DC,* precaval vein or sinus ; *Cl,* region of the cloaca ; *H,* sinus
venosus of heart ; *J,* subintestinal vein ; *Jr.V,* interrenal vein ; *Lb,* hepatic
veins ; \*\*, hepatic sinus ; *Npf,* renal portal system ; *VP,* hepatic portal vein ;
*Vpo,* capillaries of the hepatic portal system ; †, cardinal sinus ; *Sbc,* sub-
clavian vein ; *Os, Od,* left and right omphalo-mesenteric veins.

the precaval sinus or proximal end of the posterior cardinal
vein.

The caudal vein usually bifurcates posteriorly to the cloaca, each
branch passing along the outer side of the corresponding kidney,
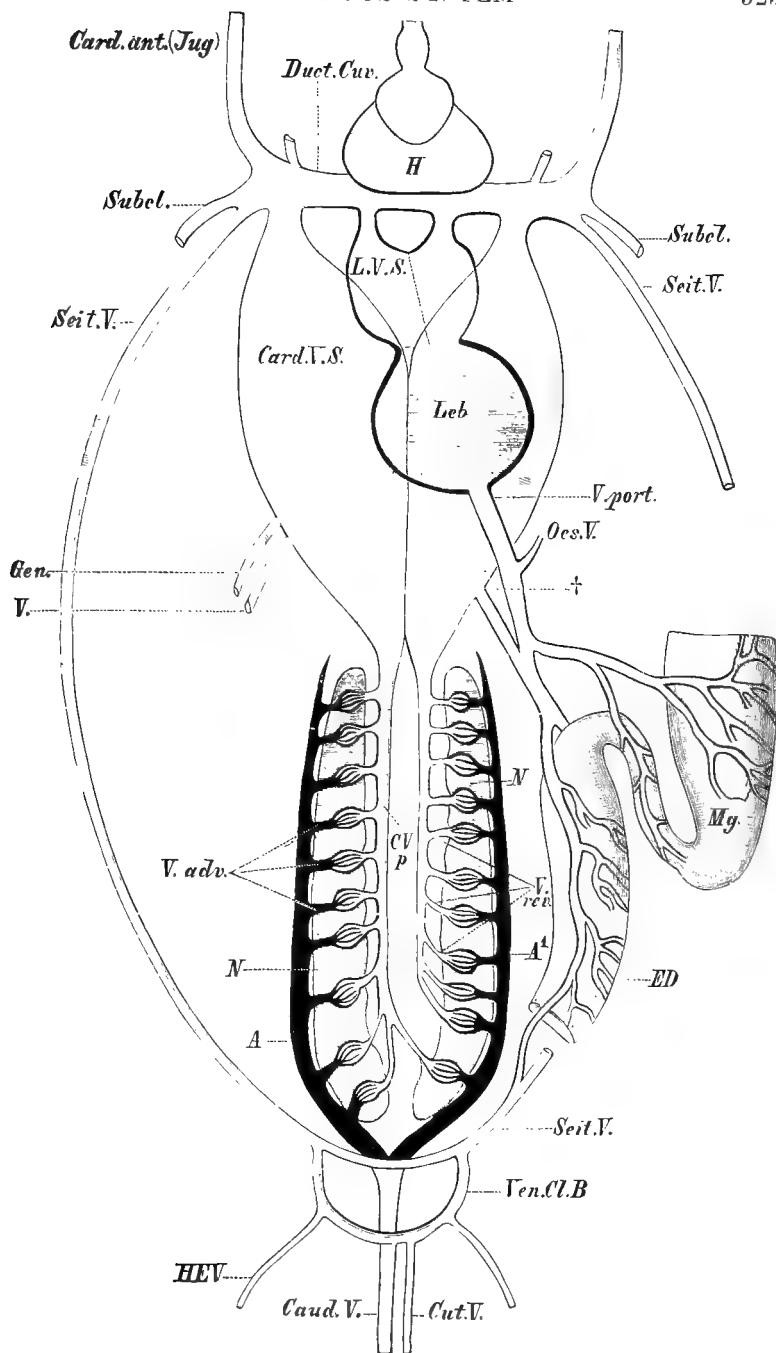
Fig. 266.—For description see next page.

Fig. 266.—Diagram of the Veins of an Elasmobranch.

*H*, heart ; *Duct.Cuv*, precaval sinus ; *Card.ant (Jug)*, anterior cardinal (jugular) ;
the inferior jugular is seen nearer the middle line ; *Subcl*, subclavian ; *Seit.
V*, lateral vein, which arises from a venous network in the region of the
cloaca (*Ven.Cl.B*), from one or more cutaneous veins of the tail (*Cut.V*),
from the veins of the body-walls, and from those of the pelvic fins
(*HEV*) ; *Caud.v*, caudal vein, which divides into two renal portals, *A*, *A*¹,
at the posterior end of the kidneys (*N*) : from these arise the adve-
hent veins of the renal portal system (*V.adv*) ; *V.rev*, revehent renal
veins, from which the posterior cardinals (*CV*) arise ; *Card.V.S*, cardinal
sinus, communicating with its fellow in the middle line ; *V.port*, hepatic
portal vein, receiving its blood from the intestine (*ED*), stomach (*Mg*), and
œsophagus (*Oes.V*), and anastomosing with the lateral vein posteriorly, and
with the cardinal sinus anteriorly ; *Gen.V*, genital veins ; *L.V.S*, hepatic
sinus ; *Leb*, liver.

and giving off advehent vessels into the latter (Figs. 264, 265, IX
—XII, 266–268).    These divide up into capillaries, forming a *renal
portal system*, the capillaries again uniting to form revehent veins
which open into the posterior cardinals.    Thus the typical condition
of the veins seen in adult Fishes is reached, and only a few of the
more important modifications can be mentioned here.

In Cyclostomes and Elasmobranchs, the anterior part of the
subintestinal vein still persists as a small vessel running within
the spiral valve of the intestine.    In the latter Order, many of the
veins (*e.g.*, precavals, anterior and posterior cardinals, inferior jugulars,
hepatic and genital veins) enlarge to form capacious *sinuses*, and
a large *lateral vein* (Figs. 264, 266), running in the body-walls either
close to the skin or just external to the peritoneum, opens into each
precaval or posterior cardinal.    This probably corresponds to the
vein of the primary lateral-fin folds (p. 104).

A renal portal system is said to be absent in Cyclostomes, and
is inconstant and very variable amongst Ganoids and Teleosts : in
many instances the caudal vein communicates directly with one or
with both posterior cardinals, and in the former case the other
cardinal shows a tendency to become reduced in size : a similar
reduction occurs in many of the forms to be described next.

**Dipnoi**.—The chief point of interest as regards the veins of
Dipnoans (Fig. 267) is the presence of a large unpaired *postcaval
vein*, derived in part from the posterior cardinal, and comparable to
that of the Amphibia and Amniota.    A renal portal system is
present, and the blood from the kidneys is collected into two veins
having the relations of posterior cardinals.    Only the left of these
however, opens anteriorly into the corresponding precaval, the
right, which is much the larger of the two, passing along the
dorsal border of the liver to open independently into the sinus
venosus in the middle line.    The renal portion of this vein is
evidently homologous with the corresponding part of the posterior
cardinal, the anterior portion of which can no longer be recognised.
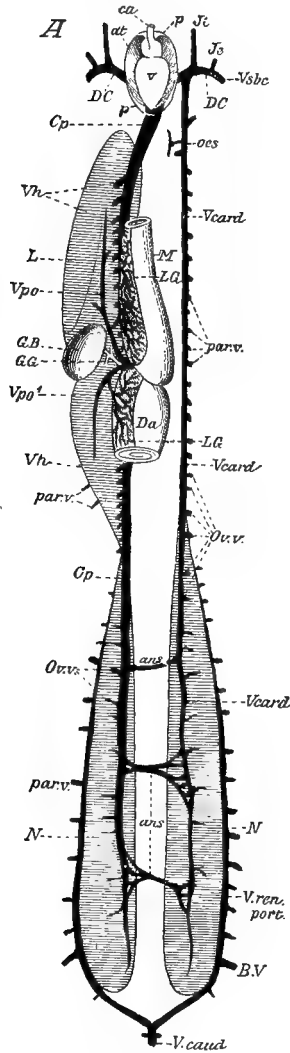
Fig. 267.—Diagram of the Venous System of *Protopterus annectens*.
(After W. N. Parker.)

*v*, ventricle ; *at*, atrium ; *p*, pericardium ; *ca*, conus arteriosus ; *Ji, Je*, internal
and external jugular ; *Vsbc*, subclavian ; *DC, DC'*, precaval veins ; *Cp*, post-
caval ; *Vh, Vh*, hepatic veins ; *L*, liver ; *G.B*, gall-bladder ; *G.G*, bile-duct ;
*M*, "stomach"; *Da*, intestine ; *L.G*, lymphoid organ in the walls of the
stomach, the blood from which passes into the hepatic portal veins (*Vpo,
Vpo¹*) ; *par.v*, parietal veins, from the body-walls ; *Ov.v*, ovarian veins ;
*N, N*, kidneys ; *BV*, pelvic vein ; *V.caud*, caudal vein ; *V.ren.port*, renal
portal vein ; *œs*, œsophageal vein ; *V.card*, left posterior cardinal vein, which
is connected by anastomoses (*ans*) with the postcaval (*Cp*) in the region of
the kidneys.

Thus the postcaval is made up of a posterior or renal portion, and of an independently developed anterior or hepatic portion.

In Ceratodus, the posterior cardinal and postcaval are directly continuous with the caudal vein, and the renal portal, receiving branches from the posterior end of the body, arises from the iliac vein, which also gives off a pelvic branch. The latter unites with its fellow in the middle line to form a median *abdominal vein*, comparable to that of the Amphibia, and opening into the sinus venosus.

The two pulmonary veins unite into a single trunk before opening into the left atrium (p. 309).

**Amphibia.**—A large postcaval vein arises in essentially the same manner as in the Dipnoi, its renal section being formed by the fusion of the two posterior cardinals in this region. The hepatic portion apparently arises in part from the right omphalo-mesenteric vein, and in part independently, while the hepatic portal vein is developed from the left omphalo-mesenteric. The postcaval receives blood from the kidneys and generative organs, as well as indirectly from the posterior extremities, body-walls, and tail (when present). The anterior part of *both* posterior cardinals persists in Urodeles and in Bombinator as the paired *azygos vein*, and this may exceptionally be present on one or both sides in other Anurans. It communicates with the corresponding precaval (Fig. 268).

A renal portal system is present, and is formed, as in Fishes, by the bifurcation of the caudal vein, which is wanting in adult Anura; into the renal portal open the veins from the hind-limb, and vessels from the body-wall often also communicate with it. The blood from the kidneys passes into the postcaval. Connecting the right and left renal portals (or femorals) is a transverse *pelvic vein*, from which, in the medio-ventral line of the body, an *abdominal* or *epigastric vein* arises, as in Ceratodus: this is primitively paired, and corresponds genetically with the lateral veins of Elasmobranchs; it extends forwards in the ventral body-wall into the liver, in which it breaks up into capillaries, becoming secondarily connected by anastomoses with the hepatic portal vein (Fig. 268). The abdominal vein receives blood from the cloaca, bladder, and body-walls. In Urodeles remains of the subintestinal vein also open into the hepatic portal system.

The arrangement of the anterior cardinals (external and internal jugulars) is essentially similar to that seen in Fishes and Dipnoans.

**Amniota.**—The section of the right posterior cardinal vein in the region of the embryonic kidney (mesonephros, p. 341) gives rise, as in the Dipnoi, to the hinder part of the postcaval: the hepatic section of the latter arises as in Amphibia. In the Sauropsida, the anterior portions of both posterior cardinals disappear,
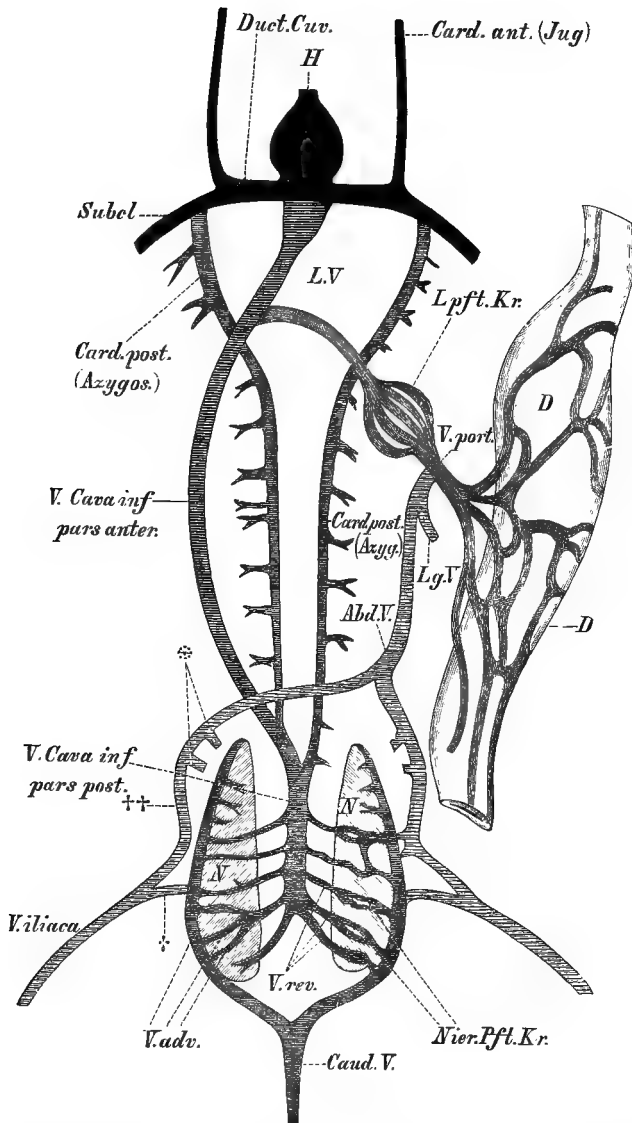
FIG. 268.—Diagram of the Venous System of *Salamandra maculosa*.

*Caud. V*, caudal vein, which bifurcates at the posterior end of the kidneys (*N, N*) to form the renal portal system (*Nier. Pft. Kr*); *V. adv*, *V. rev*, advehent and revehent renal veins; *V. iliaca*, femoral vein, which divides into an anterior (††) and a posterior (†) branch: the latter opens into the renal portal, and the former (pelvic vein) unites with its fellow to form the abdominal vein (*Abd. V*), and also receives vessels (*) from the cloaca, bladder, and posterior part of the intestine. *V. Cava inf. pars anter*, and *V. Cava inf. pars poster*, anterior and posterior sections of the postcaval; *Card. ant (Jug)*, and *Card. post (Azyg)*, anterior and posterior cardinal veins (*i.e.*, the jugular and azygos). *Subcl*, subclavian vein; *Duct. Cuv*, precaval; *H*, heart; *D, D*, alimentary canal, from which the hepatic portal vein (*V. port*) arises; *Lg*, longitudinal vein of the intestine; *Lpft. Kr*, hepatic portal system; *L.V*, hepatic vein.

and are replaced by *vertebral veins*, while in Mammals, they persist as the *azygos veins*. An anastomosis is formed between these, and eventually the anterior part of the left disappears, the blood from both sides passing into the right azygos (hemiazygos), which opens into the right precaval (Figs. 269 and 270).

The anterior cardinals give rise, as in lower Vertebrates, to the jugulars, which, as well as the subclavians and vertebrals or azygos,
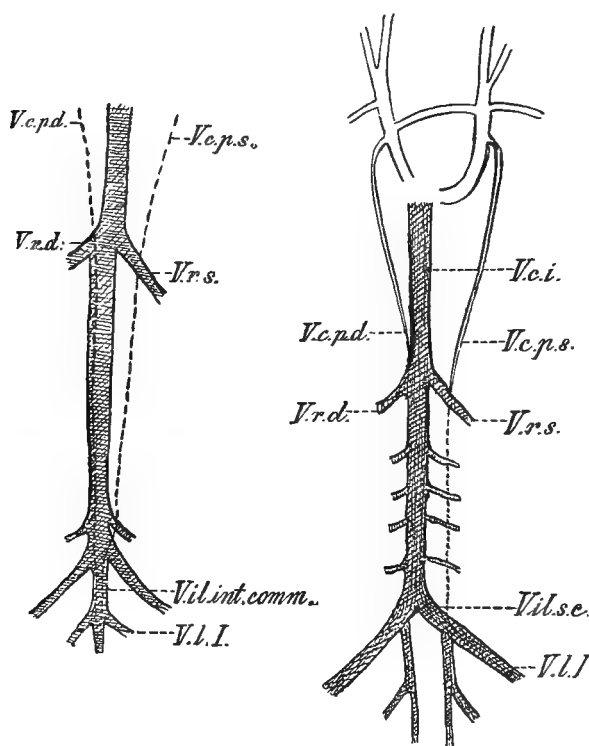


FIG. 269.—DIAGRAM SHOWING THE RELATIONS OF THE POSTERIOR CARDINAL AND POSTCAVAL VEINS IN A, THE RABBIT, AND B, MAN. (After Hochstetter).

*V.r.d*, *V.r.s*, renal veins ; *V.cl.s.e*, common iliac vein ; *Vl.I*, lumbar vein ; *V.c.i*, postcaval ; *V.c.p.d*, *V.c.p.s*, right and left posterior cardinals ; *V.il.int.comm*, common internal iliac vein.

open into the precavals. In Reptiles, Birds, Monotremes, and Marsupials, as well as in many Rodents, Insectivores, Bats, and Ungulates, both precavals persist throughout life ; but in other Mammals the main part of the left disappears, all the blood from the head and anterior extremities passing into the right. The coronary veins open into the base of the left precaval (coronary sinus, Fig. 259).

A renal portal system occurs in connection with the embryonic kidney in all Sauropsida, and traces of it can also be recognised in embryos of Echidna. In adult Reptiles, renal portal veins give off branches into the permanent kidney (metanephros, p. 346): in
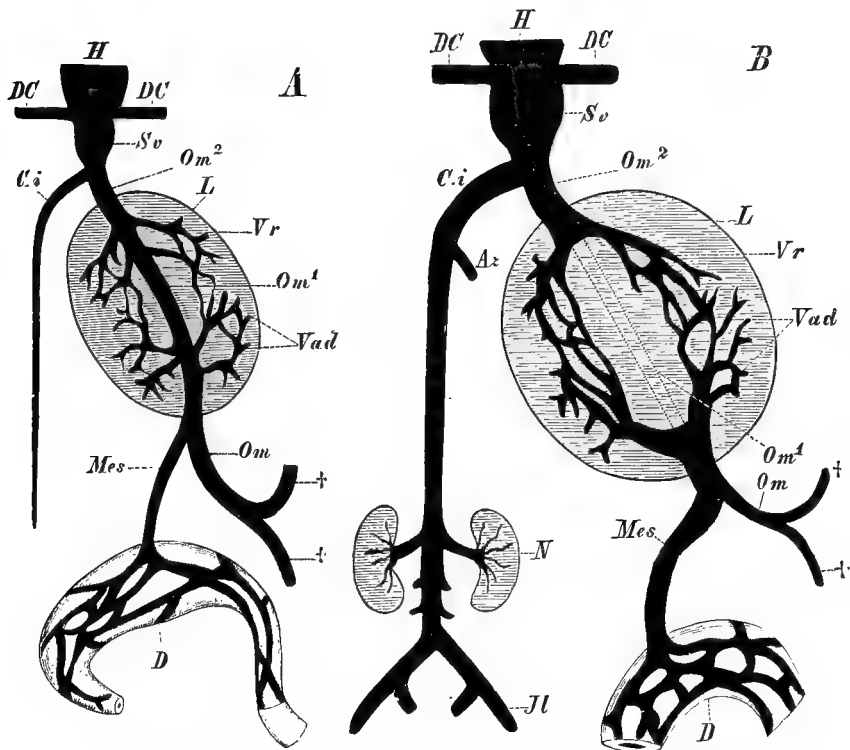


FIG. 270.—DIAGRAM ILLUSTRATING THREE STAGES IN THE DEVELOPMENT OF THE HEPATIC PORTAL SYSTEM.   (See next page for c.)

$H$, heart; $Sv$, sinus venosus; $DC$, $DC$, precavals; $Ci$, postcaval; $L$, liver; $Om$, $Om^1$, $Om^2$, the three sections of the omphalo-mesenteric vein (the first still shows its originally paired nature at ††: in stage $B$, the second section of this vein, which passes through the liver, disappears, so that $Om$ and $Om^2$ are only connected by capillaries: in stage $C$, the first section ($Om$) has quite disappeared, and the umbilical vein ($Umb$) has become developed); $DA$, ductus venosus; *, connection of the umbilical vein with the capillaries of the liver; $Vr$, revehent veins; $Vad$, advehent veins; $Mes.$, mesenteric vein, which later gives rise to the hepatic portal ($V.port$), receiving blood from the alimentary canal ($D$); $Az.$, azygos; $Jl$, iliac vein; $N$, kidney.

Birds only a slight indication of such a renal portal system exists, and in Mammals it is entirely wanting.

As in Fishes, the first veins to appear in the embryo are the omphalo-mesenteric veins (Fig. 270, A), bringing back the blood from

the yolk-sac, and uniting into a single trunk before opening into the heart. As the liver becomes developed, a portal circulation arises, and the main trunk of the vein, where it passes through the liver, disappears. In the meantime, the cœliac and mesenteric veins have become developed, and all the blood from them, as well as from the vitelline veins, now passes through a common trunk, the hepatic portal vein, into the capillaries of the liver, whence it
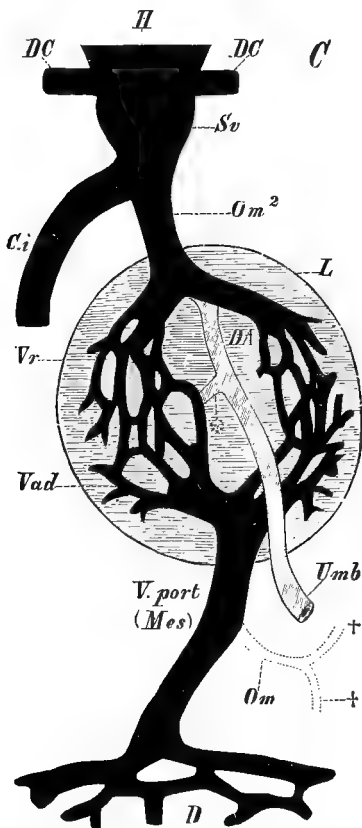


Fig. 270, c.—Reference to lettering on previous page.

reaches the sinus venosus through the hepatic veins. The vitelline veins gradually disappear as the yolk-sac becomes reduced.

In addition to these vessels, the *umbilical vein* must also be mentioned. This vessel is originally paired, and corresponds genetically to the lateral veins of Elasmobranchs and to the abdominal or epigastric vein of Ceratodus and Amphibians. It is situated originally in the body-walls, and comes into relation with the allantois (pp. 9 and 337), opening eventually into the

postcaval : as the allantois increases in size, it brings back the oxygenated blood from this organ (*i.e.*, from the placenta in the higher Mammalia). The right umbilical vein, however, early becomes obliterated, and the left comes into connection with the capillaries of the liver, its main stem in this region disappearing (Fig. 270, B). Thus the blood from the allantois has to pass through the capillaries of the liver before reaching the heart. In the course of development, however, a direct communication is formed between the left umbilical vein and the remains of the fused vitelline veins, and this trunk is known as the *ductus venosus* (Fig. 270, c). On the cessation of the allantoic (or placental) circulation, the ductus venosus becomes degenerated into a fibrous cord, so that all the portal blood has to pass through the capillaries of the liver.

The intra-abdominal portion of the umbilical vein persists throughout life as the epigastric vein in Reptiles and in Echidna, but disappears in Birds and in other Mammals.

The mode of development of the veins of the extremities is essentially similar in all the Amniota, and at first resembles that occurring in Amphibia, though later on considerable differences are seen in these two groups, more especially as regards the veins of the digits.

### Retia Mirabilia.

By this term is understood the sudden breaking-up of an arterial or venous vessel into a cluster of fine branches, which, by anastomosing with one another, give rise to a capillary network ; the elements of this network may again unite to form a single vessel. The former condition may be described as a *unipolar*, the latter as a *bipolar* rete mirabile. If it is made up of arteries or of veins only, it is called a *rete mirabile simplex*; if of a combination of both kinds of vessels, it is known as a *rete mirabile duplex*.

The retia mirabilia serve to retard the flow of blood, and thus cause a change in the conditions of diffusion. They are extremely numerous throughout the Vertebrate series, and are found in the most varied regions of the body, as, for instance, in the kidneys (glomeruli, p. 345)—where their above-mentioned function is most clearly seen ; on the ophthalmic branches of the internal carotid ; on the vessels of the air-bladder in Fishes (p. 280); along the intercostal arteries of Cetacea ; on the portal vein ; and along the caudal portion of the vertebral column in Lizards.

### Lymphatic System.

In Fishes, Amphibians, and Reptiles, but more particularly in the first-named Class, *lymph vessels* (p. 299) are often not plainly differentiated, and occur mainly along the great blood-

vessels, as well as on the bulbus arteriosus and ventricle, lying in the connective-tissue surrounding these structures. Numerous independent lymphatic vessels may, however, also be present, arising from a capillary network under the skin, and extending into the intermuscular septa; the intestinal tract and the viscera are also generally provided with definite lymph-vessels in the Amphibia and Amniota.

Contractile *lymph-hearts* may be present in connection with the vessels. They occur in Fishes, but are much better known in Amphibians, Reptiles, and Bird-embryos. Thus, in Urodeles, numerous lymph-hearts are present under the skin along the sides of the body and tail, at the junction of the dorsal and ventral body-muscles; in other Amphibians they are either confined to the posterior end of the body (pelvic region), or, as in the Frog, are present also between the transverse processes of the third and fourth vertebræ. In Reptiles posterior lymph-hearts only are present, and are situated at the boundary of the trunk and tail regions, close to the transverse processes or ribs. Similar structures are not known to be present in Mammals.

Large lacunar *lymph-sinuses* are present under the skin of tailless Amphibia, and the skin is thus only loosely attached to the underlying muscles. These subcutaneous lymph-sinuses are connected with those of the peritoneal cavity. Amongst the latter, the *subvertebral lymph-sinus* is of great importance in Fishes, Dipnoans, and Amphibians; it surrounds the aorta and is connected with the (mesenteric) sinus lying amongst the viscera, into which the lymphatic vessels of the intestine open. In Fishes and Dipnoans there is also a large longitudinal lymphatic trunk lying within the spinal canal.

As already mentioned, the higher we pass in the animal series the more commonly are lymphatic trunks with independent walls to be met with. From Birds onwards a large longitudinal subvertebral trunk (the *thoracic duct*) is always present. In Mammals this arises in the lumbar region, where it is usually dilated to form the *cisterna* or *receptaculum chyli*; it receives the lymph from the posterior extremities, the pelvis, and the urinogenital organs, as well as the *lacteals*, or lymphatics of the intestine. In Mammals it communicates anteriorly with the left, and in Sauropsida with both left and right precaval veins. The lymphatics of the head, neck, and anterior extremities open into the same veins.

The lymphatic vessels of Birds and Mammals are, like certain of the veins, provided with *valves*, the arrangement of which allows the lymph stream to pass in one direction only, *i.e.*, towards the veins.

The lymph, as already mentioned (p. 299), consists of two elements, a fluid (*plasma*) and cells (*lymph-corpuscles, leucocytes*); and similar cells are present in the *lymphoid* or *adenoid tissue* which occurs beneath the mucous membrane in various parts of the body ·

(*e.g.*, alimentary canal, bronchi, conjunctiva, urinogenital organs) and is particularly abundant in Fishes, Dipnoans, and Amphibians (pp. 267, 352, 363).

The migration of the amœboid leucocytes to the surface (p. 267) is due to various causes. It may simply result in getting rid of superfluous material, or may be of considerable importance in removing broken-down substances and harmful bodies (*e.g.*, inflammatory products, Bacteria), the particles being ingested by leucocytes (hence often called *phagocytes*) before the latter are got rid of.

The mass of lymphoid tissue on the heart of the Sturgeon, and possibly also the so-called fat-bodies (*corpora adiposa*) of Amphibia and Reptilia (pp. 368, 370), and the "*hibernating gland*" of certain Rodents, may be placed in this category ; they consist of lymphoid and fatty tissue, and serve as stores of nutriment.

The agglomeration of a number of lymphoid follicles gives rise to those structures which are spoken of as "*lymphatic glands*" or *adenoids*. These are always interposed along the course of a lymphatic trunk so that afferent and efferent vessels to each can be distinguished. They probably appear first in Birds, and are most numerous in Mammals, where they are present in abundance in various regions of the body ; they differ greatly in size.

The *spleen* which is present in almost all Vertebrates, is closely related to these structures. It corresponds to a specially differentiated portion of a tract of lymphoid tissue primarily extending all along the alimentary canal, and in Protopterus it still remains enclosed within the walls of the stomach (Fig. 209). In other Vertebrates it is situated outside the walls of the canal, but even then may extend along the greater part of the latter (*e.g.*, Siren). Usually, however, either the proximal or the distal portion of it undergoes reduction, and the organ is generally situated near the stomach, though it is occasionally met with in other regions of the intestinal tract, as, for instance, at the commencement of the rectum (Anura, Chelonia). In some cases (*e.g.*, Sharks) it is broken up into a number of smaller constituents.

The *tonsils* are also adenoid structures. They are most highly developed in Mammals, where they give rise to a paired organ lying on either side of the fauces—that is, in the region where the mouth passes into the pharynx, and usually also to a mass situated more posteriorly on the walls of the pharynx itself (pharyngeal tonsils) ; the latter are phylogenetically the older organs and are present in Reptiles, Birds, and most Mammals.[1] The tonsils consist of a retiform (adenoid) connective-tissue ground-substance enclosing a number of lymph-corpuscles, which are arranged in so-called *follicles*, and are capable of migrating to the surface.

[1] Tonsil-like organs are also present in Amphibians.

New leucocytes are continually formed in the marrow of the bones, as well as in the lymphatic glands and spleen; the spleen is apparently also of importance in absorbing the broken-down remains of the red blood-corpuscles.

## MODIFICATIONS FOR THE INTER-UTERINE NUTRI-
## TION OF THE EMBRYO: FŒTAL MEMBRANES.

### I. ANAMNIA.

IN several **Elasmobranchs** the oviduct gives rise to glandular villi which secrete a nutritive fluid, and in an Indian Ray (Pteroplatea micrura) there are specially long glandular villiform processes which extend in branches through the spiracles into the pharynx of the embryos, of which there may be as many as three in each oviduct. The gill-clefts of the embryos are in close apposition, and there are no gill filaments (see p. 278).

In certain viviparous Sharks (viz., Mustelus lævis and Carcharias) the walls of the vascular yolk-sac become raised into folds or villi, which fit into corresponding depressions in the walls of the oviduct, the latter becoming very vascular. A kind of *umbilical placenta* is thus formed, by means of which an interchange of nutritive, respiratory, and excretory matters can take place between the maternal and fœtal blood-vessels.

Amongst viviparous **Teleosts** (comp. p. 360) various arrangements for the nutrition of the embryo occur. In Zoarces viviparus (and probably also in the Embiotocideæ), the embryos are retained in the hollow ovary, the empty follicles (corpora lutea) of which give rise to extremely vascular villi, from which a serous fluid containing blood- and lymph-cells is extruded into the cavity of the ovary and thus surrounds the masses of embryos. These swallow the fluid and digest the contained cells. In other forms (*e.g.*, viviparous Blennies, and Cyprinodonts), the embryos undergo development within the vascular follicles, and are probably nourished by diffusion; while in Anableps, villi are developed from the yolk-sac, and these doubtless absorb the nutritive fluid from the walls of the ovary.

In certain **Amphibians** which have no prelarval existence, interesting modifications occur for nourishing the young until the larval stage is passed. Thus in the Alpine Salamander (Salamandra atra), a large number of ova (40—60) pass into each oviduct, just as in the allied S. maculosa, in which the young are born as gilled larvæ. Were this the case in S. atra, the young would be carried away in the mountain streams and destroyed, and a curious adaptive modification has therefore arisen in this form, in

which only one embryo (that nearest the cloaca) in each oviduct undergoes complete development, remaining within the body of the parent until the gills are lost and metamorphosis has taken place.    The other eggs break down and form a food-mass for the survivors after their own yolk has become used up.    Degenerative changes, moreover, take place in the epithelium of the oviduct, and masses of red blood-corpuscles pass into the lumen of the latter, undergo degeneration, and become mixed with the broken-down yolk-masses, the resulting broth being swallowed by the surviving young.    After the birth of the latter, the uterine epithelium becomes regenerated ; and thus a process occurs which somewhat resembles that of the formation of a *decidua* in placental Mammals (p. 340).

## II.  Amniota.

In all the Amniota, as already mentioned (pp. 9 and 302), fœtal membranes, known as the *amnion* and *allantois* are developed, the latter, or primary urinary bladder, represented only in rudiment in the Amphibia (p. 259), being of great importance in connection with respiration, secretion, and (in the higher Mammals) nutrition of the embryo.

A glance at Fig. 8 will show that, owing to its mode of development, the amnion[1] consists primarily of two layers ; an inner, the *amnion proper*, and an outer or *false amnion*.    The latter lies close to the vitelline membrane, and forms the so-called *serosa*, or *serous membrane*.    As the allantois grows it extends into the space continuous with the cœlome between the true and false amnion, and may entirely surround the embryo.

Amongst **Reptiles,** the eggs of the viviparous Lizard, Seps chalcides, are relatively poor in yolk, and this is compensated for by the yolk-sac and allantois coming into close relation with the walls of the oviduct, thus forming an *umbilical* and an *allantoic placenta*, one at either pole of the embryo ; the latter of these is the more important.    Both fœtal and maternal parts of the placentæ become extremely vascular, and thus the necessary interchange of materials can take place between the blood of the embryo and mother.    In Trachydosaurus and Cyclodus, as well as in the Chelonia, a kind of umbilical placenta is apparently also formed.

The fact that a vascular yolk-sac (often known as the *umbilical vesicle*) is present in placental **Mammals,** indicates that they are descended from forms in which, like the Sauropsida, the eggs were rich in yolk, and which were viviparous.    This condition is

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[1] As the head enlarges and sinks downwards, it is at first surrounded by a modification of the head fold (p. 9) consisting entirely of epiblast and called the *pro-amnion* : this is afterwards replaced by the amnion.

moreover retained in the Monotremes, and even in Marsupials the ova are relatively large as compared with those of the higher Mammalia.

As the amount of yolk gradually became reduced in the course of phylogenetic development, close relations were set up between the fœtal (allantoic) and maternal blood-vessels, the allantois becoming closely applied to the serosa to form a *chorion* (Fig. 271); but that this condition was only very slowly evolved is shown by the fact that, even at the present day, Mammals exist in which it has not been reached. These (viz., Monotremes and most Marsupials) are therefore known as *Aplacentalia* or *Achoria*, in contradistinction to the higher *Placentalia* or *Choriata*. Moreover, in the Rodentia, Insectivora, Cheiroptera, Carnivora, and Ungulata more or less distinct indications of an *umbilical placenta*, formed in connection with the yolk-sac, can still be observed, and at a still earlier stage the ova are nourished by uterine lymph (compare p. 336).



FIG. 271.—DIAGRAM OF THE FŒTAL MEMBRANES OF A PLACENTAL MAMMAL. (From Boas's *Zoology*.)

*al*, allantois; *am*, amnion; *b*, yolk-sac (umbilical vesicle); the outermost line represents the serous membrane. The outer wall of the allantois has united with the serous membrane to form the chorion from which branchial villi arise.

In Monotremes and Marsupials, both the yolk-sac and allantois take part in respiration; in the former the two are of equal importance, while amongst the latter the yolk-sac is solely or mainly (Phalcolarctos) important in this respect. In Perameles obesula a further approach towards the formation of a true *allantoic placenta* is seen, the allantois giving rise to small vascular villi. In most Marsupials the allantois serves merely as a urinary reservoir, and in none of them does it possess any important function as an organ of nutrition, the young being born at a relatively early stage, when they become attached to the teats of the mother, and are then nourished by means of milk (see p. 288).

In the higher Mammals, the umbilical placenta has usually only a very temporary importance, though in some cases (*e.g.*, Rodents) it probably takes some part in respiration and nutrition during the whole uterine life. The allantois extends out from the body of the embryo and becomes attached to the serous membrane to form the chorion, from which numerous villi extend into the uterine wall (Fig. 271). As both the latter and the allantois become extremely vascular, the uterine and allantoic capillaries and sinuses coming into close contact with one another, a complicated

allantoic placenta arises, consisting of maternal and fœtal parts (Fig. 9). Thus the embryo is supplied with the necessities for existence during its comparatively long intra-uterine life.

Various forms of placenta are met with amongst the Placentalia. The most primitive type is apparently that in which the allantois becomes attached around the whole serosa, so that the resulting chorion, from which the comparatively simple villi arise, are equally distributed over the whole surface (Fig. 271). This form is known as a *diffused placenta*, and is met with in Manis, the Suidæ, Hippopotamus, Tylopoda, Tragulidæ, Perissodactyla, and Cetacea.

The next stage is characterised by the chorionic villi becoming more richly branched, so as to present a greater superficial extent, and at the same time being concentrated into definite and
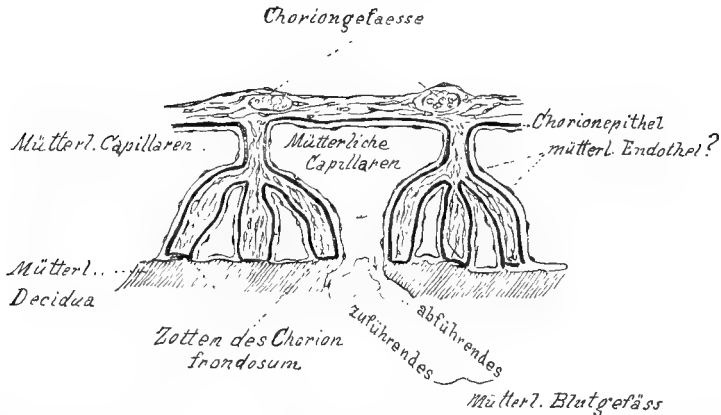


FIG. 272.—DIAGRAM TO ILLUSTRATE THE RELATIONS OF THE FŒTAL AND MATERNAL VESSELS IN THE HUMAN PLACENTA, SHOWING CHORIONIC AND MATERNAL VESSELS AND CAPILLARIES, VILLI (*Zotten*), AND DECIDUA. (After Keibel.)

more or less numerous patches or cotyledons. Thus a *polycotyledonary* placenta arises, such as is met with in most Ruminants, some of which, such as Cervus mexicanus and the Giraffe, show an interesting intermediate form of placenta between the diffuse and the cotyledonary.

The chorionic villi in these two types of placenta, even though more or less branched, separate from the uterine mucous membrane at birth, the latter not becoming torn away : these placentæ are therefore spoken of as *non-deciduate*.

A further complication is seen in the forms of placenta known as the *zonary*, the *dome-* or *bell-shaped*, and the *discoidal*, in which the connection between fœtal and maternal parts becomes much more close, the villi giving rise to a complicated system of branches within the uterine mucous membrane (Fig. 272). Thus the latter

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becomes to a greater or less extent torn away at birth (*decidua*), the placenta being therefore spoken of as *deciduate*. In these cases, the placental part of the chorion does not extend all round the embryo. In the zonary placenta only the two opposite poles of the chorion are more or less free from vascular villi, and this girdle-like form occurs in the Carnivora, as well as in the Elephant Hyrax, and Orycteropus. In Lemurs and Sloths, the placenta is dome- or bell-shaped, while in Myrmecophaga, Dasypodidæ (Armadilloes), and Primates (Fig. 9) it forms a discoidal mass on the dorsal side of the embryo (metadiscoidal form). The discoidal placenta of Rodentia, Insectivora, and Cheiroptera has probably not arisen, like that just mentioned, from a diffused type, but was originally restricted to a discoidal area, owing to the umbilical vesicle occupying a large surface of the chorion.

From the above description it is evident that the differences in the form of the placenta are mainly those of degree, and that the latter gives little indication of the systematic position of the animal in question.

The histological structure of the placenta and the various modifications seen in the maternal mucous membrane cannot be described here ; it is, however, important to note that there is no direct communication between the maternal and fœtal blood, and that the maternal capillaries usually enlarge to form sinuses, the walls of which become invaginated by the villi : thus the latter are covered by an epithelium furnished by the maternal tissues (Fig. 272).

In the course of development the embryo becomes more and more folded off from the yolk-sac (Fig. 8), the stalk of which latter and that of the allantois, enveloped by the base of the amnion, together form the *umbilical cord*. At birth, the fœtal membranes are shed, the intra-abdominal portion of the allantois persisting as the urachus (comp. p. 358).

# I. URINOGENITAL ORGANS.

## *a.* GENERAL PART.

The first traces of the urinary and generative organs of Verte-
brates arise on the dorsal side of the cœlome, right and left of the
aorta, and are more or less closely connected with one another,
both morphologically and physiologically.

The part of the urinogenital system first to arise is the paired
**pronephros** and its duct, the **pronephric duct.** This is the
most ancient and primitive excretory organ of Vertebrates; it is
usually restricted to a few of the anterior body segments, close
behind the head, whence it is often known as the "head-kidney."
It originates primarily as a series of segmentally arranged
invaginations of the somatic mesoblast in the region of the ventral
section of the mesoblastic somites, these invaginations giving rise
to *excretory tubules* or *nephridia* (Figs. 273 and 274); secondarily,
however, in consequence of alterations in the relative rate of
growth of the parts, the tubules come to arise in connection with
the unsegmented body-cavity. Each tubule opens into the cœlome
by a ciliated funnel or *nephrostome,* and comes into relation with a
segmental blood-vessel which primarily connects the aorta with the
subintestinal vein. These vessels become coiled to form a rete
mirabile known as the *glomus* (Fig. 274). Primarily, as in Chæto-
pods, the tubules must have opened at the other end on to the
surface independently, through the ectoderm (Fig. 277, A, and comp.
Amphioxus, p. 348 and Figs. 219 and 277, A), but this condition is
no longer observable in the Craniata, in which they all communi-
cate with a longitudinal pronephric duct. The number of nephro-
stomes is in most cases not more than two or three.

The pronephric duct is apparently a later acquisition than the
pronephros itself. It first appears in the somatic mesoblast,[1]
arising by the fusion of the peripheral ends of the pronephric
tubules to form a longitudinal collecting tube (Figs. 274, 277, B),
which extends backwards to open into the cloaca, thus establishing
a communication between the cœlome and the exterior.

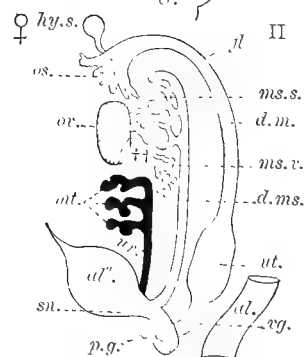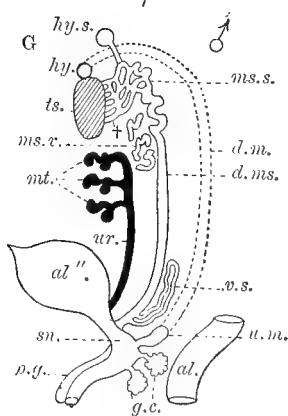[1] In Elasmobranchs its origin can be traced to the epiblast.
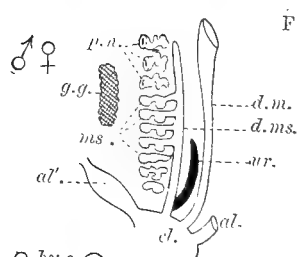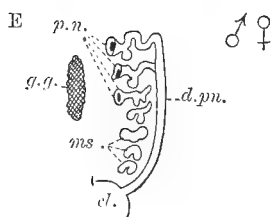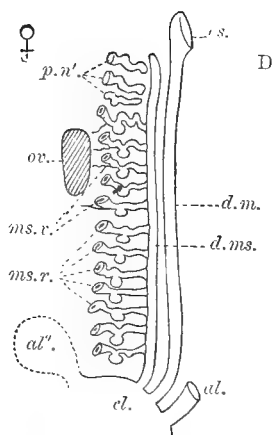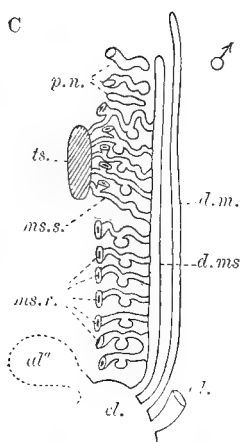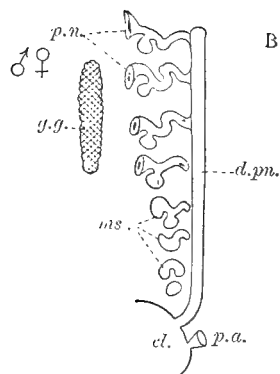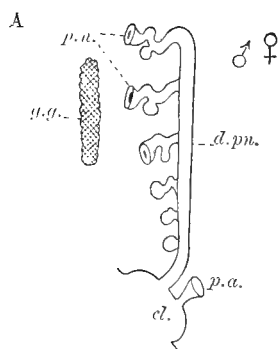
FIG. 273.—A SERIES OF DIAGRAMMATIC FIGURES ILLUSTRATING THE ACCOUNT OF THE COMPARATIVE MORPHOLOGY OF THE URINOGENITAL ORGANS OF THE VERTEBRATA GIVEN IN THE FOLLOWING PAGES.

A, the pronephros stage of the Anamnia; B, a later stage of the same; C, the urinogenital apparatus of the male Amphibian; D, the same of the female; E, pronephros stage of the Amniota, the mesonephros as yet rudimentary; F, urinogenital apparatus of the Amniota at a stage at which the sexes are not differentiated; G, urinogenital apparatus of male Amniota; H, the same of female Amniota.

*p.n.*, pronephros; *d.pn.*, duct of the pronephros; *ms.*, the developing mesonephros; *ms.s*, part of the mesonephros, becoming converted into the epididymis and parovarium; *ms.r*, vestiges of the mesonephros, the paradidymis and the paroophoron; †, rete and vasa efferentia testis; ††, a network homologous with these structures at the hilum of the ovary; *hy.s*, stalked hydatid; *ms.z*, portion of the mesonephros which in Amphibians and Elasmobranchs becomes the so-called pelvic kidney; *d.ms*, duct of the mesonephros, which in male Amphibians and Elasmobranchs becomes (Fig. C) the urinogenital, and in females (Fig. D) the urinary duct. In the male Amniota it gives rise to the seminal duct (Fig. G), and in the female to Gärtner's duct (Fig. H); *r.s*, the seminal vesicle, an outgrowth of the duct of the mesonephros; *d.m.*, Müllerian duct, which in Mammals becomes differentiated (Fig. H) into the Fallopian tube (*fl*), the uterus (*ut*), and the vagina (*vg*); *vs*, its abdominal aperture; *hy*, and *u.m* (Fig. G), unstalked hydatids and uterus masculinus (vestiges, in the male, of the Müllerian duct, *d.m.*); *m.t.*, the definitive kidney or metanephros of the Amniota, said to arise from the ureter (*ur*), itself an outgrowth of the mesonephric duct; *al*, allantois or urinary bladder; *su*, urinogenital sinus; *p.g*, genital prominence, *g.g*, gonads, undifferentiated stage; *ov*, ovary; *ts.*, testis; *cl*, cloaca; *al*, rectum; *p.a*, abdominal pore; *g.c*, Cowper's glands.

TABULATED RÉSUMÉ OF THE FACTS PICTORIALLY ILLUSTRATED ON THE OPPOSITE PAGE.

| | | Anamnia. | Amniota. |
|---|---|---|---|
| Pronephros. | Male and Female. | Develops in all Anamnia, but rarely persists as a permanent excretory organ. | Still develops in the Amniota, but as an excretory organ undergoes entire degeneration in the embryo: it may take part in the formation of the suprarenal body (?) |
| Duct of Pronephros. | Male and Female. | In Elasmobranchii, appears to give origin by subdivision to both mesonephric (Wolffian) and Müllerian ducts. In Amphibia, becomes converted into the mesonephric duct. Its fate in other Anamnia is not yet fully investigated. | Probably persists as the mesonephric (Wolffian) duct, and contributes in some to the formation of the Müllerian duct. |
| Mesonephros. | Male and Female. | Functions in all Anamnia as a urinary gland. In Elasmobranchs, Amphibians, and one or two higher Fishes, its anterior portion becomes related to the male genital apparatus, the posterior portion persisting as a permanent kidney. | Loses its renal function in all Amniota (as a rule in the embryo), and becomes vestigial, except so far as it becomes an accessory portion of the reproductive apparatus in the male and enters into the formation of the suprarenal body (?) |

TABULATED RÉSUMÉ—(*Continued*).

| | | Anamnia. | Amniota. |
|---|---|---|---|
| **Mesonephros.** | Male. | The proximal portion becomes in most cases (except in Cyclostomes and Teleosts) related to the testis and functional in the transmission of the semen, the distal functioning as a kidney. | The proximal end becomes the rete and vasa efferentia testis, the caput epididymis, and perhaps also the stalked hydatid of Morgagni : the distal end becomes the paradidymis (Giraldé's organ). |
| | Female. | Persists as the kidney. | The greater part of the proximal portion becomes the parovarium, the distal the paroophoron. |
| **Duct of Mesonephros.** | Male. | Functions in most higher Fishes merely as the urinary duct.<br>In Elasmobranchs, Amphibians, and some Ganoids, serves as the urinogenital duct. | The proximal portion becomes the corpus and cauda epidymis and the distal the seminal duct (vas deferens). |
| | Female. | Functions exclusively as the duct of the mesonephros, *i.e.*, the urinary duct. | The greater part, as a rule, degenerates ; the proximal portion may be retained in a vestigial form in the region of the parovarium. In certain cases it may persist, as a whole, as Gärtner's canal. The distal end becomes the organ of Weber. |
| **Müllerian Duct.** | Male. | In Elasmobranchs it degenerates in post-embryonic life, vestiges of its proximal portion being retained. Its existence in most other Fishes is doubtful. In Dipnoi and Amphibia it is retained, at any rate for some time, for its whole length, in a functionless and often but little degenerate condition. | The proximal portion becomes the unstalked hydatid of Morgagni, the distal, in some Mammals, the so-called "uterus masculinus." In exceptional cases the whole is retained as Rathke's duct. In Sauropsida the distal part usually disappears. |
| | Female. | When present, becomes the whole genital duct. | Becomes the whole genital duct. |
| **Metanephros and Ureter.** | Male and Female. | Probably unrepresented (comp r. 352). | Appears to arise in part (ureter) from the distal end of the mesonephric duct, and in part (secreting elements) as a caudal extension of the mesonephros. |

The pronephros itself has only a transitory function as an excretory organ. Its duct, however, always persists, and usually undergoes important modifications, which are closely connected with the appearance of a second and more extensive series of
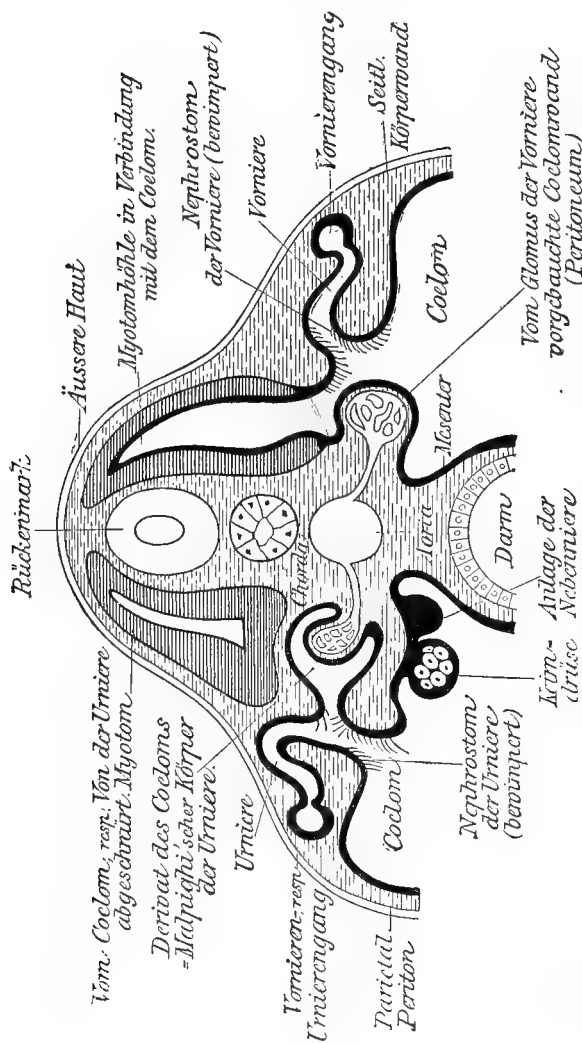


FIG. 274. DIAGRAMMATIC TRANSVERSE SECTION ILLUSTRATING THE PRIMARY RELATIONS OF THE PRONEPHROS (ON THE RIGHT) AND MESONEPHROS (ON THE LEFT) WITH THEIR DUCTS.

In the middle line are seen, from above downwards, the spinal cord, notochord, aorta, and intestine. On the right the cavities of the myotome and the cœlome are seen to be continuous, and a pronephric tubule (*Vorniere*), the pronephric duct (*Vornierengang*), and the glomus are shown. On the left, the cavity of the myotome has become shut off from the cœlome, and a mesonephric tubule (*Urniere*) and its duct, as well as a Malpighian capsule are shown. Between the ciliated nephrostome of the mesonephric tubule and the intestine are seen the rudiments of the gonad (*Keimdrüse*) and suprarenal (*Nebenniere*).

excretory segmental tubules, which appear later, mainly posteriorly to the pronephros, and constitute the **mesonephros** or mid-kidney; the pronephric duct now serves as a **mesonephric duct.**

The mesonephros, often known as the *Wolffian body* (Figs. 273, 274, 277, B), is sometimes regarded as corresponding simply to

a "later generation" of pronephric tubules. It appears more probable, however, that this organ originates independently from a part of the mesoblastic somites situated more dorsally than that which gives rise to the pronephric tubules. Primitively, the mesonephros is strictly metameric, owing to the fact that each of its tubules corresponds to the primary channel connecting the cavity of a somite with the unsegmented cœlome (Fig. 274). The loss of connection between these two sections of the primary cœlome results in a series of segmental nephridia, each of which opens into the body-cavity by a nephrostome, while at its other, or blind end, it comes into connection with the pronephric duct—or mesonephric duct as it must now be called (Fig. 275). The glomus of the pronephros is continued backwards, and in the region of the mesonephros breaks up into portions, or *glomeruli,* each of which is situated in a small cavity constricted off from the cœlome and opening into a mesonephric tubule, forming what is known as a *Malpighian capsule* (Figs. 274, 275).



FIG. 275.—DIAGRAM OF THE MESONEPHRIC TUBULES, SHOWING THEIR (SECONDARY) CONNECTION WITH THE MESONEPHRIC DUCT (*SG*).

The two anterior tubules are already connected with the duct, while the two posterior have not yet reached so far. *ST,* nephrostome; *M,* Malpighian capsule with glomerulus; *DS,* coiled glandular tubule; *ES,* terminal portion of latter.

Each mesonephric tubule, then, in its primitive form, is made up of the following portions (Fig. 275):—(1) a funnel-shaped ciliated aperture, communicating with the body-cavity (*nephrostome,* or *peritoneal funnel*); (2) a rounded mass of capillaries (*glomerulus*), which is situated within a cavity (*Malpighian capsule*) derived from the cœlome; and (3) a coiled *glandular tubule,* opening into a collecting (mesonephric) duct. Thus the mesonephros, as well as the pronephros, besides its main function of excreting waste products by means of the epithelial cells lining the tubules, serves also to conduct water derived from the blood in the glomeruli, and peritoneal fluid, from the body.

The mesonephros is of greatest importance in the Anamnia : in many Fishes it serves exclusively as a urinary organ, but in Elasmobranchs and higher forms it also takes on certain relations to the generative apparatus, giving rise to the *rete* and *vasa efferentia* of the testis, as well as to the *parorchis* or *epididymis* (p. 350), and, in Amniota, to other more or less rudimentary organs of secondary importance (compare Fig. 273). Nevertheless, it may still serve as the permanent urinary organ (Elasmobranchs, Amphibians), or may more or less entirely disappear as such (Amniota); in the latter case, a third series of tubules is formed, giving rise

to a **metanephros,** or hind-kidney, with which is connected a **metanephric duct** or **ureter.**

The metanephros corresponds to a later developed posterior section of the mesonephros. Each metanephric duct apparently arises as a hollow outgrowth from the posterior end of the mesonephric duct, where the latter opens into the cloaca. It gradually extends forwards, and comes into connection with a series of tubules developed as buds from the hinder end of the mesonephros and provided with cœlomic Malpighian capsules and with glomeruli, but not with nephrostomes. The posterior end of the ureter soon loses its connection with the mesonephric duct, and opens independently either into the cloaca or into a urinary bladder (Figs. 294—297).

### The Male and Female Generative Ducts.

In the Elasmobranchii, Amphibia, and Amniota, *two* canals are formed in connection with the primary excretory apparatus : one of these is known as the *secondary mesonephric* or **Wolffian duct**—which in male Elasmobranchii and Amniota functions as a seminal duct or *vas deferens* and in male Amphibia as a urinogenital duct, and the other as the **Müllerian duct**—which opens anteriorly into the cœlome and serves in the female as an *oviduct* (Figs. 278, 279). The Wolffian duct becomes rudimentary in the female—except in Amphibians, in which it still serves as a urinary duct (Fig. 279)— and the Müllerian duct remains in a more or less rudimentary condition in the male. These two ducts in some cases (Elasmobranchs) arise by a splitting of the primary mesonephric duct into two (Fig. 278), but more usually the Müllerian duct arises independently from the cœlomic epithelium. All the urinogenital ducts are lined by a mucous membrane, external to which are muscular and connective tissue layers. (For the relations of the urinary and generative ducts in other Fishes and in Dipnoans see pp. 360–363.)

### The Gonads (" Generative Glands ").

The **sexual cells,** which give rise to the *ova* and *spermatozoa* originate from the **germinal epithelium,** which corresponds to a differentiation of part of the cœlomic or peritoneal epithelium on the dorsal side of the body-cavity on either side of the mesentery, and into which the adjacent mesoblastic stroma penetrates ; thus a pair of **gonads** or "sexual glands" is formed (Fig. 274).

Primitively the gonads were arranged segmentally, and extended throughout a greater number of body segments (compare Amphioxus, p. 359).

The primitive germinal cells are at first entirely undifferentiated, but in the course of development a differentiation takes place, resulting in the formation of a male or a female gonad, *i.e.,* a **testis** or an **ovary.**

The mode of development of the ova and spermatozoa is briefly as follows :—

*Ova.*—The cells of the germinal epithelium grow inwards amongst the stroma of the ovary in the form of clustered masses : some of these increase in size more than the others, and give rise to the *ova*, while the smaller cells form an investment of *follicle* round them, and serve as nutritive material. The investing cells multiply, and in Mammals a cavity containing a fluid is formed in the middle of each follicle (Fig. 276) : the main mass of the follicular cells which enclose the ovum project, as the *discus proligerus*, into the cavity of the follicle. When ripe, the ovum, surrounded by a vitelline membrane, comes to the surface of the ovary and breaks through into the abdominal cavity ; it then passes into the cœlomic aperture of the oviduct. A certain amount of blood is poured out through the broken ends of the vessels in the stroma of the ovary into the cavity of the follicle in which the ovum lay : this " wound " then closes up, and its contents undergo fatty degeneration, giving rise to a body of yellow colour, known as the *corpus luteum.*

*Spermatozoa.*—As in the case of the female, primitive germinal cells can be at first distinguished in the development of the male generative elements. These give rise to a series of *seminal tubules* (Fig. 300), containing larger and smaller cells ; the former undergo division to form the sperm-cells or
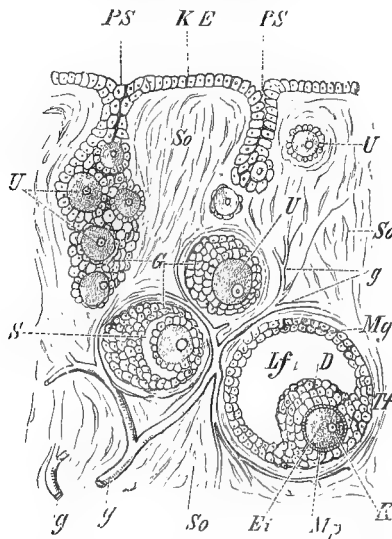


FIG. 276.—SECTION THROUGH A PORTION OF THE OVARY OF A MAMMAL, SHOWING THE MODE OF DEVELOPMENT OF THE GRAAFIAN FOLLICLES.

*KE*, germinal epithelium, ingrowths from which extend into the stroma of the ovary to form the ovarian tubes (*PS*) : the stroma is penetrated by vessels (*g.g*); *U, U*, primitive ova ; *S*, cavity between the follicular epithelium (tunica granulosa, *Mg*) and the primitive ova ; *Lf*, liquor folliculi ; *D*, discus proligerus ; *Ei*, ripe ovum, with its germinal vesicle (*K*) and germinal spot ; *Mp*, zona pellucida, showing radiated structure ; *Tf*, theca folliculi.

spermatozoa. The nucleus gives rise to the so-called " head " of the spermatozoon, while the surrounding protoplasm becomes differentiated to form the motile " tail," which serves as an organ of propulsion, the " neck " (Mittelstück) arising from the centrosome of the cell (p. 3).

## b. SPECIAL PART.

### Urinary Organs.

In **Amphioxus** a series (90 or more) of independent segmental tubules are present on either side in the reduced section of the cœlome situated on the dorsal side of the pharynx (" dorsal
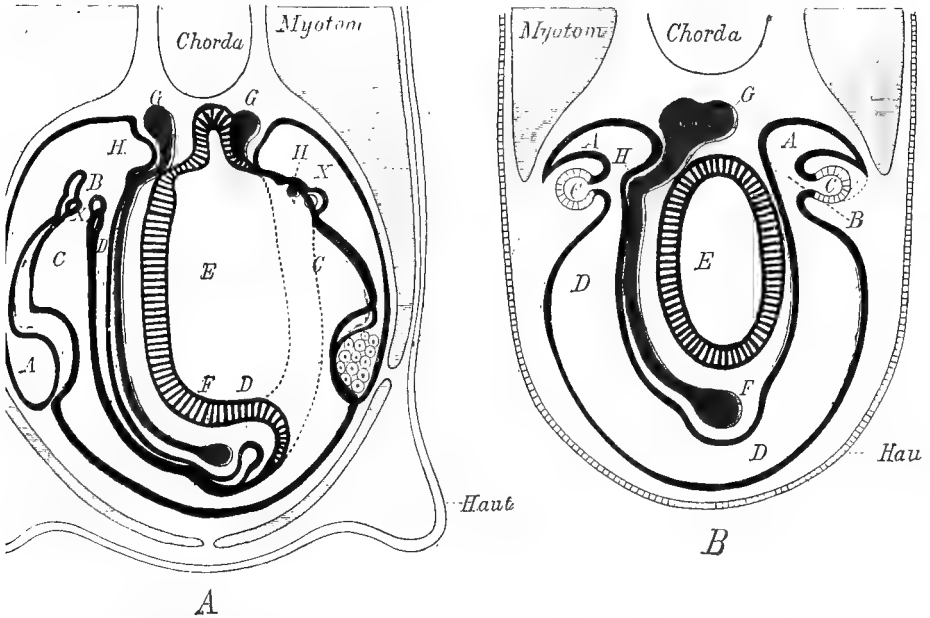


Fig. 277.—Diagrammatic Transverse Sections through A, Amphioxus, in the Branchial Region, and B, an Elasmobranch Embryo, based on Boveri's Figures.

*In* A, the section passes through a branchial cleft on the right side, and shows a transverse section of the anterior limb of a nephridium (*X*) ; on the left, a nephridium (*X*) is indicated showing its communication with the cœlome (*B*) and with the atrial chamber (*C*). *A*, genital section of cœlome (an ovary is indicated on the right side) ; *D*, section of the cœlome which extends down the branchial bars ; *F*, ventral aorta.

*In* B, the section represents the pronephric region on the left, and the meso-nephric region on the right. *A*, rudiment of a mesonephric tubule, the blind end of which subsequently comes to open into the pro- (or meso-) nephric duct (*C*) as indicated by the dotted lines on the right. *B*, nephro-stome ; *D*, cœlome : *F*, subintestinal vein.

*In both figures*, *E*, lumen of gut ; *G*, aorta ; *H*, portion of commissural vessel which comes into relation with the excretory system.

cœlomic canals "). Each of these tubules comes into close relation with a branchial blood-vessel, possesses a varied number of lateral branches, and opens on the one hand into the cœlome by several ciliated funnels or nephrostomes, and on the other by a single aperture into the atrial or peribranchial chamber (p. 275), which

thus also serves as an excretory duct (Figs. 219 and 272, A). The segmental arrangement of the tubules in the adult corresponds to that of the branchial apparatus, and not to that of the myotomes. No nephridia are present posteriorly to the pharynx, and it is possible that the excretory system of Amphioxus may be to a certain extent comparable to an early stage of the pronephros of the Craniata.

In **Cyclostomes** the pronephros persists beyond the larval period, and for some time at any rate, functions as the sole excretory organ : it possesses three or four nephrostomes. In Petromyzon it is soon replaced by a mesonephros, and the pronephros then becomes rudimentary : between the two a fat-body is situated. In Myxine it is uncertain whether the whole kidney, or only its anterior part, represents the pronephros. The kidney does not come into relation with the generative organs, and its duct, which opens on either side into the urinogenital sinus, probably represents the unaltered pronephric duct.

In the **Teleostei** the pronephros has, in the majority of cases,[1] only a temporary significance, and the mesonephros constitutes the excretory organ of the adult : it consists of a narrow band varying in size and diameter in different regions, situated on the dorsal side of the body-cavity, between the vertebral column and the air-bladder. Secondary fusions between the organ of either side often occur. The urinary duct in both groups probably represents the pronephric duct, and may lie more or less freely, or be embedded in the substance of the kidney. Posteriorly the two ducts usually fuse together and become expanded to form a kind of urinary bladder (compare Figs. 286 and 287) which has nothing to do with the allantoic bladder of Amphibia and Amniota. The bladder usually opens behind the anus—either independently or together with the genital ducts—by a simple pore, or on the summit of a urinogenital papilla.

Thus a differentiation of the pronephric (or primary mesonephric) duct into a Wolffian and a Müllerian duct is not known to occur in Teleostei, nor does the mesonephros come into connection with the gonads ; in **Elasmobranchii**, in which the pronephros is more rudimentary, this differentiation takes place (p. 346), and at the same time a distinction between an anterior and a posterior section of the mesonephros may be observed (compare Figs. 278, 289, and 290). In the male, the former (*parorchis* or *epididymis*) comes into connection with the testis by means of small ducts, the *vasa efferentia*, and its tubules open directly into the Wolffian duct, which thus functions as a vas deferens only ; while the latter, which persists as the permanent kidney, empties its secretion by means of separate urinary ducts into the base of the Wolffian duct. In the female the Wolffian

[1] It is said to persist in *Fierasfer, Lophius, Dactylopterus, Orthagoriscus mola, Mora mediterranea,* and the *Macruridæ.*
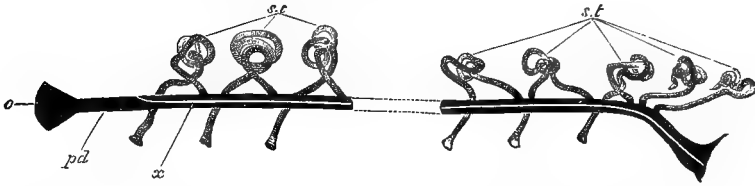
FIG. 278A.—DIAGRAM OF THE PRIMITIVE CONDITION OF THE KIDNEY IN AN
ELASMOBRANCH EMBRYO. (After Balfour.)

*pd*, pronephric duct : it opens at *o* into the body-cavity, and its other extremity
communicates with the cloaca ; *x*, line along which the division appears which
separates the pronephric duct into the Wolffian duct above, and the Müllerian
duct below ; *s.t*, nephridial tubes : they open at one end in the body-cavity,
and at the other into the Wolffian duct.
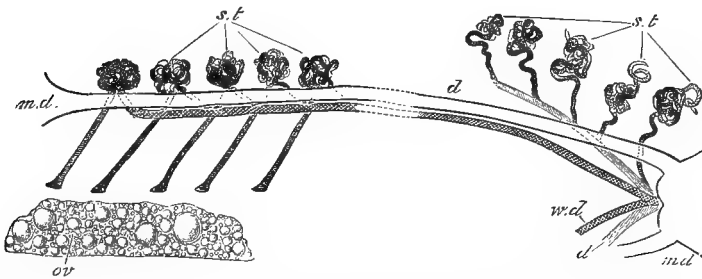


FIG. 278B.—DIAGRAM OF THE ARRANGEMENT OF THE URINOGENITAL ORGANS IN
AN ADULT FEMALE ELASMOBRANCH. (After Balfour.)

*m.d*, Müllerian duct ; *w.d*, Wolffian duct ; *d*, urinary duct ; *s.t*, nephridial tubes :
five of them are represented with openings into the body-cavity : the posterior
nephridial tubes form the functional kidney ; *ov*, ovary.
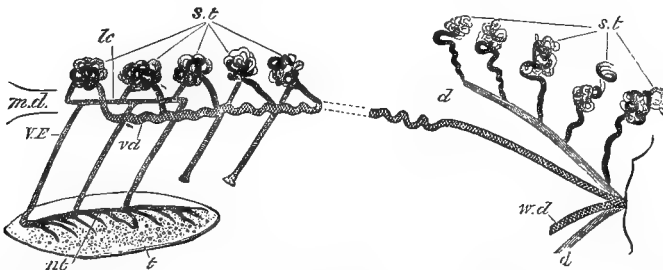


FIG. 278C.—DIAGRAM OF THE ARRANGEMENT OF THE URINOGENITAL ORGANS IN
AN ADULT MALE ELASMOBRANCH. (After Balfour.)

*m.d*, rudiments of Müllerian duct ; *w.d*, Wolffian duct, marked *vd* in front, and
serving as vas deferens ; *s.t*, nephridial tubes : two of them are represented
with openings into the body-cavity : the anterior tubules give rise to the
parorchis or epididymis and the posterior ones to the functional kidney ; *d*,
urinary duct ; *t*, testis ; *nt*, canal at the base of the testis ; *VE*, vasa
efferentia ; *lc*, longitudinal canal of the Wolffian body.

duct is rudimentary, and the ova pass to the exterior by means of the Müllerian duct.

This special differentiation of the hinder part of the meso-nephros, and the formation of special ducts in connection with it, seems to foreshadow the condition which occurs in the Amniota (pp. 346 and 356).

The anterior (sexual) part of the kidney is usually broader than the posterior (renal) part. The outer border is usually notched, and this, together with the arrangement of the nephrostomes in the embryo, points to the original segmental arrangement of the organ. The segmental character, however, disappears later on ; in the adult the nephrostomes are much less numerous than the vertebræ of this region, but their number and size vary much in different genera and even in individuals, and they apparently do not persist in all.

The morphology of the kidneys and renal ducts in **Ganoids** (Figs. 286 and 287) requires further investigation. They seem on the whole to resemble those of Teleosts, though in the Sturgeon they apparently show points of similarity to those of Elasmobranchs. As in the Teleostei, a well-developed pronephros is present in the larva, and the kidney duct probably represents the pronephric duct.

In many Fishes the kidneys extend far back into the root of the tail.

A close examination of the organ, which appears to the naked eye as the kidney in Teleosts and Ganoids, shows that a larger or smaller portion of it —more particularly the anterior part—consists of an adenoid or lymphoid substance.

In the **Dipnoi** the kidneys also undoubtedly correspond to the mesonephros. They are relatively longer in Protopterus (Fig. 288) than in Ceratodus, extending through a considerable portion of the body-cavity : as in Elasmobranchs, a narrower anterior can be distinguished from a broader posterior part, and the whole is largely invested by lymphoid and adipose tissue. Nephrostomes are wanting. Until their development is known, it is uncertain to what extent the renal ducts correspond to the primary mesonephric ducts : each opens into the cloaca inde-pendently, behind the genital aperture. The cloacal cæcum (p. 262) probably functions as a urinary bladder.

**Amphibia.**—The pronephros is well developed in the larva, and is particularly large in the Gymnophiona, in which as many as 12 or 13 nephrostomes may be present.

In adults, the most primitive condition is met with in the Gymnophiona, in which the kidney (mesonephros) consists of long, narrow, varicose bands, usually extending from the heart to the anterior part of the cloaca, which latter is often much elongated. In the embryo they consist of definite masses, which are arranged metamerically, and in each of them a glomerulus, a nephrostome, and an excretory duct can be distinguished (Fig. 291). This con-dition sometimes persists in the anterior portion of the kidney,

but, owing to secondary processes of growth, as many as twenty nephrostomes are later on met with in a single body-segment. The number of nephrostomes in the entire kidney may amount to a thousand or more.

As regards the urinary duct and the relations of the entire
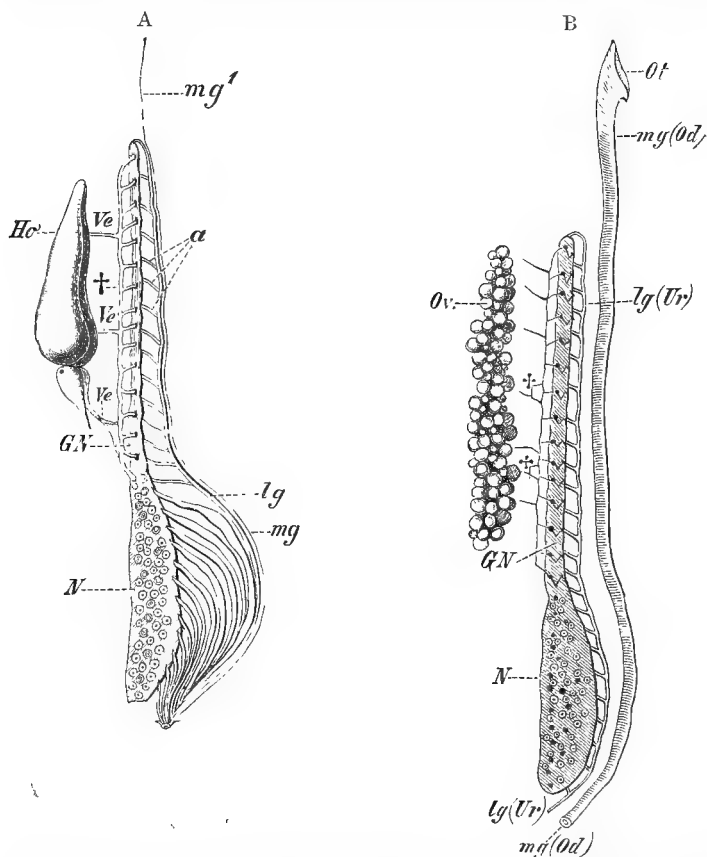


Fig. 279.—Diagram of the Urinogenital System of (A) a Male and (B) a Female Urodele; founded on a Preparation of *Triton taeniatus*. (After J. W. Spengel.)

*Ho*, testis; *Ve, Ve*, vasa efferentia of testis, which open into the longitudinal canal of the mesonephros, †; *a*, collecting tubes of the mesonephros, which open into the Wolffian (urinogenital) duct (*lg, lg*); in the female the latter serves simply as the urinary duct (*Ur*), and the system of the vasa efferentia (testicular network) is rudimentary; *mg, mg*[1] (*Od*), Müllerian duct; *Ot*, cœlomic aperture of latter in the female; *Ov*, ovary; *GN*, anterior sexual portion of kidney (parorchis of the male); *N*, posterior non-sexual portion of kidney.

renal apparatus to the generative organs, the Gymnophiona in all essential points resemble other Amphibia.

The kidneys of Urodela and Anura are situated in the usual position on the dorsal side of the body-cavity; in the former they are band-like and more extended longitudinally than in the latter,

A A

in which they are shorter and more compact, and are confined to the middle portion of the cœlome.

In Urodeles they always consist of a narrow anterior, and a broader and more compact posterior portion. The latter, as in Elasmobranchs, gives rise to the functional kidney (Fig. 279), while the former becomes connected in the male with the generative organs. Delicate vasa efferentia, developed from the mesonephros, pass out from the testis (Figs. 279, 280, 292) into the substance of the kidney, and there open into the renal tubules; they may either enter the kidney direct, or else open first into a longitudinal collecting duct, from which fine canals pass to the tubules. Thus the seminal fluid passes through the nephridia as well as through the Wolffian duct, which serves as a urinogenital duct.
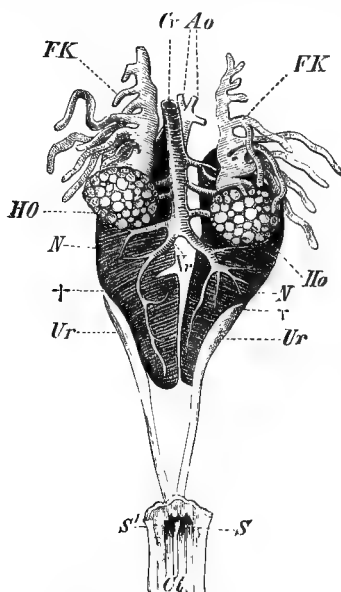


Fig. 280.—Male Urinogenital Organs of *Rana esculenta*.

*Ur, Ur,* Urinogenital (Wolffian) ducts, which appear on the lateral surface of the kidneys at †; *S, S',* their apertures into the cloaca (*Cl*) ; *Ho, Ho,* testes ; *FK, FK,* corpora adiposa ; *Cv,* postcaval vein ; *Ao,* aorta ; *Vr,* revehent renal veins.

In Urodela and Anura of both sexes the Wolffian duct nearly always opens separately on either side into the cloaca, receiving first, in Urodeles, a number of ducts from the posterior part of the kidney (compare Elasmobranchs, p. 350). In Anura the Wolffian ducts pass some distance independently along the body-cavity, in correspondence with the position of the kidneys, and a seminal vesicle opens into each (Fig. 281).

The *urinary* (allantoic) *bladder* (see p. 259) opens into the cloaca ventrally, opposite to the urino-genital apertures. In its simplest form it is finger-shaped (*e.g.,* Siren, Proteus), but it usually becomes swollen distally and is often bi-lobed : in Alytes and Bombinator it forms a double sac.

Slight indications of a seg-mental arrangement are found only in the anterior sexual portion of the kidney of Urodeles; in the posterior part, and in the entire kidney of Anura, all traces of segmentation have disappeared. In both cases, however, the nephrostomes remain throughout life in great numbers on the ventral surface of the kidney, which is covered over by the peritoneum (Fig. 281).

The nephrostomes are connected with the urinary tubules in larval Anura, but later on they become separated from them, and open into the renal
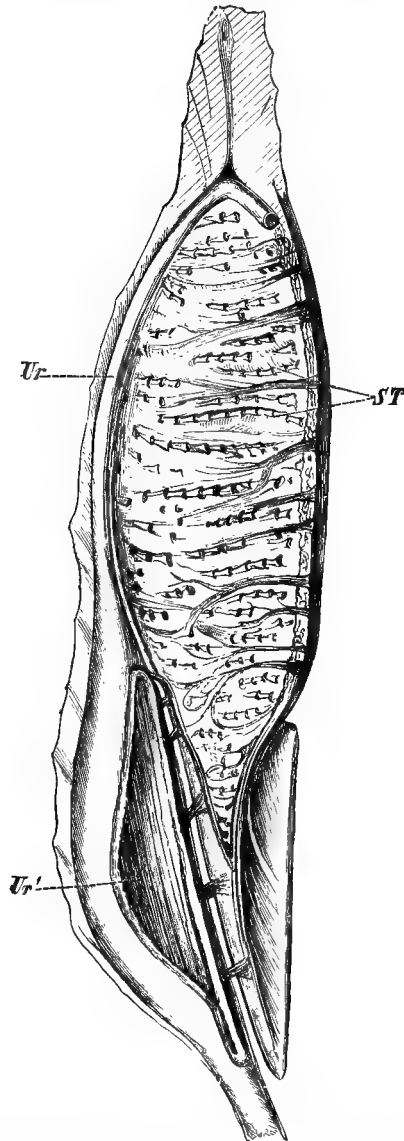
FIG. 281.—KIDNEY OF *Discoglossus pictus*. From the ventral surface, showing the nephrostomes (*ST*). (After J. W. Spengel).

*Ur*, urinogenital duct, enlarging at *Ur* [1] to form a seminal vesicle.

veins. In consequence of this change of function, for such it must be considered, the body-cavity of adult Anura forms a closed lymph-sinus, as in the Amniota ; the peritoneal fluid, which in the larva was carried to the exterior and lost, is in the adult poured into the general circulation, like the rest of the lymph.

**Reptiles and Birds.**—In the Sauropsida, as in the Mammalia, the mesonephros, so far as it is retained in the adult, is entirely separate from the functional excretory apparatus; this consists of a metanephros, entirely wanting in nephrostomes (compare p. 346 and Fig. 273).

The metanephros never extends so far along the body-cavity as does the mesonephros; as a rule it has the form of a small compact or lobulated organ, usually situated in the posterior half of the body-cavity, or even entirely confined to the pelvic region: it has the latter position, for instance, in most Reptiles
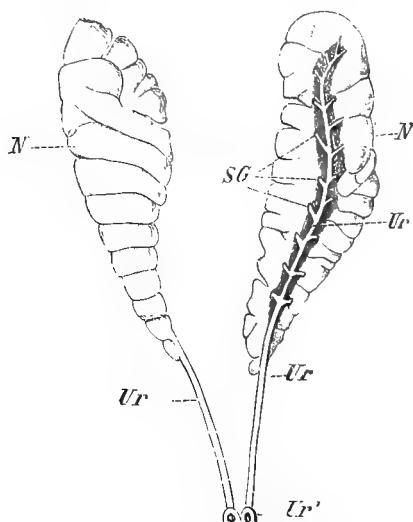


FIG. 282.—EXCRETORY APPARATUS OF *Monitor indicus*.

The right kidney is shown in its natural position, while the left is turned on its longitudinal axis, so that the ureter and the collecting tubes are visible. The urinary bladder is not represented.

*N*, *N*, kidneys; *SG*, collecting tubes which open into the ureter (*Ur*, *Ur²*); *Ur¹*, aperture of ureter into the cloaca.

(Figs. 282, 294 and 295) and all Birds (Fig. 283). The posterior end of the kidney, which is generally narrower than the rest, may even extend under the root of the tail, as in Lacerta, in which region there is a fusion of the organ of either side.

Thus, according to the position of the kidneys, the ureters (metanephric ducts) either do not extend freely along the body-cavity, or they may have a longer or shorter free course. The latter is the case, for instance, in Crocodiles, and more especially in Birds (Fig. 283): in the latter the kidneys are closely embedded within the pelvis, and their ventral flattened surface, which is usually divided into three lobes, is

often penetrated by deep furrows and clefts in which the veins lie embedded; posteriorly they may fuse together in the middle line, as in Lizards.

There is not always a perfect symmetry between the organ of either side, and this is most marked in Snakes, in which the
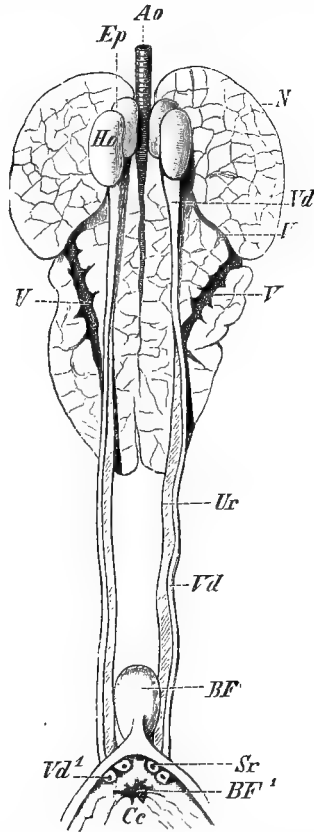


FIG. 283. —MALE URINOGENITAL APPARATUS OF HERON (*Ardea cinerea*).

*N*, kidneys; *Ur*, ureter, opening into the cloaca (*Cc*) at *Sr*; *Ho*, testis; *Ep*, epididymis; *Vd*, vas deferens, which opens at *Vd*[1] on a papilla in the cloaca: *V*, *V*, furrows on the ventral surface of the kidney in which veins lie embedded; *Ao*, aorta; *BF*, bursa Fabricii, which opens into the cloaca at *BF*[1].

greatly lobulated kidneys, like those of limbless Lizards, are elongated, narrow, and band-like, in correspondence with the form of the body.

A *urinary* (allantoic) *bladder* arising from the ventral wall of the cloaca, is present in Lizards and Chelonians; it is more or less bilobed. A bladder is wanting in Snakes, Crocodiles, and Birds.

**Mammals.**—The definitive kidneys (metanephros) of Mammals are proportionately small, and lie on the quadratus lumborum muscle and ribs. They usually possess a convex outer, and a concave inner border; the latter is called the *hilum*, and at this point the ureters arise and the blood-vessels enter. The expanded proximal portion of the ureter is divided up to form one or more *calyces* (Fig. 284), into which small papilliform processes of the *pyramids* (see below) project; on the summits of these the urinary tubules open in varying number. The calyces are continuous with a large cavity in the widened portion of the ureter called the *pelvis*, and from this the ureter (metanephric duct) passes freely backwards for some distance to open into the bladder (except in Monotremes, Fig. 296) on its dorsal side, sometimes nearer the apex, sometimes towards the fundus. The bladder communicates with the *urinogenital canal* or *urethra*.



FIG. 284.—DIAGRAMMATIC LONGI-
TUDINAL SECTION THROUGH THE
KIDNEY OF A MAMMAL.

*R, R,* cortical substance ; *M, M,*
medullary substance arranged in
pyramids (*Pr*) ; between the
latter the cortical substance ex-
tends in the form of the columns
of Bertini (*B, B*) ; *Ca,* calyces ;
*Pe,* pelvis ; *Ur,* ureter.

The kidney is greatly lobulated in the embryo; this condition may remain throughout life, or the lobes may become more or less completely united (Fig. 285). In the latter case the original division into lobes may still be recognised more or less plainly internally. A section of the kidney shows an inner layer, the *medullary substance,* arranged in the form of wedges—the urinary pyramids,—and an outer layer, or *cortical substance,* extending as the columns of Bertini between the pyramids (Fig. 284). The pyramids correspond roughly to the embryonic lobes of the kidney, though several lobes may fuse together in one pyramid.

The glomeruli as well as the coiled portions of the tubules, sur-rounded by a network of blood-capillaries, lie in the cortical substance, while the straight portions of the tubules extend through the pyramids, where they gradually anastomose to form larger collecting tubes.

The greater part of the *urinary bladder* does not corre-spond with the proximal end of the allantois, but to a special differentiation of the cloaca, which becomes divided into a dorsal and a ventral portion by the formation of a horizontal septum. The ventral portion gives rise to the bladder, which is continuous distally with the stalk of the allantois (urachus, see p. 340), from which the median ligament of the bladder is formed. In Monotremes and nearly all Marsupials (see

p. 338) the whole allantois takes part in the formation of the bladder.
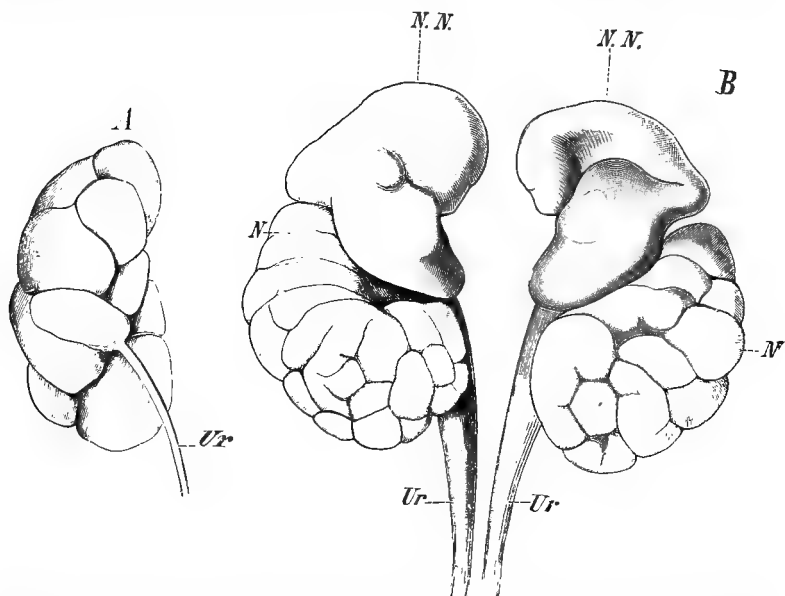


FIG. 285.—A, RIGHT KIDNEY OF A DEER ; B, KIDNEYS ($N$) AND SUPRARENAL BODIES ($N.N$) OF THE HUMAN EMBRYO. (Both from the ventral side.) $Ur$, ureters.

## GENERATIVE ORGANS.

In **Amphioxus** the gonads are developed in a part of the reduced cœlome situated on either side of the pharynx and intestine (Fig. 277, A) between the outer body-wall and the atrial cavity. They have a marked segmental arrangement, and each portion sheds its products independently into the atrial cavity, whence they pass out through the atrial pore (compare p. 275 and Fig. 219).

In **Cyclostomes** also, generative ducts are wanting ; the spermatozoa or ova are shed directly into the body-cavity, and pass through the genital pores (p. 298) into the urinogenital sinus, and so to the exterior. The gonad is a long unpaired organ suspended, as in other Vertebrates, to the dorsal wall of the body-cavity by a fold of peritoneum, the mesorchium or mesoarium, as the case may be.

In Fishes the gonads are only exceptionally unpaired, and even then, this is only a secondary condition, due to the fusion of the two organs or to the reduction of that of one side ; as in all

other Vertebrates, they are originally paired. There is usually a want of symmetry observable between the organ of the right and left sides.

The testes and ovaries of **Teleostei** closely correspond with one another as regards position and the arrangement of their ducts. Dorsal and ventral folds of the peritoneum are developed in connection with the elongated ovary, and these in most cases meet along its outer side, so as to enclose a portion of the cœlome and thus convert the ovary into a hollow sac, blind anteriorly, on the inner folded walls of which the ova arise; this sac is continued backwards to form the oviduct (compare Fig. 286). The latter, which is generally short, as a rule fuses with its fellow to form an unpaired canal; this opens either by a genital pore (p. 298) between the rectum and the urinary aperture on a level with the integument, or on a papilla, which may become elongated to form a tube or "ovipositor"; or the ducts may communicate with a urinogenital sinus.

The testis of Teleosts is elongated, and often lobulated in form. Its duct has similar relations to those seen in the female.

Thus the ducts, both of the ovary and testis, correspond to folds of the peritoneum enclosing a cœlomic cavity continuous with that of the gonads, and originate quite independently of the nephridial system. The oviducts must therefore be distinguished from true Müllerian ducts.

In some Teleosts the ovary is solid, and the ova are shed into the body-cavity. In the Smelt (Osmerus) and in Mallotus the oviducts ("peritoneal funnels") have open cœlomic apertures close to the ovaries into which the ova pass (compare Fig. 286, B); while in other Salmonidæ and in the Murænidæ and Cobitis, for instance, these peritoneal funnels are shorter, and may even be absent, the ova then being shed into the urinogenital sinus through a paired or single genital pore. It is uncertain whether the latter is the primitive arrangement amongst Teleostei, or whether the peritoneal funnels represent reduced oviducts.

Most Teleostei are oviparous, but viviparous forms occur (p. 336). The male Stickeback builds a nest for the protection of the young formed of a hardened secretion (mucin) of the kidney, which undergoes a change of function at the breeding-season ; in Syngnathus and Hippocampus the young are protected within a pouch on the abdomen of the male, and in the female Solenostoma on a pouch between the ventral fins. Amongst Siluroids they are carried within the pharynx in the male Arius, and the eggs are attached to the soft ventral integument in the female Aspredo.

Amongst **Ganoidei** the female organs of Lepidosteus are formed on the same type as those of the Teleostei. In Amia (Fig. 286, B) and Acipenser each oviduct opens by a funnel into the cœlome, but in all Ganoids the oviduct is probably comparable to that of Teleosts, and not to a Müllerian duct. In the male Lepidosteus a series of vasa efferentia pass out from the testis and

open into a longitudinal canal from which ducts pass into the
kidney, the duct of which therefore serves as a urinogenital duct
(Fig. 287). The latter dilates before uniting with its fellow to
open into the urinogenital sinus. A somewhat similar arrange-
ment appears to occur in the male Sturgeon, in which representatives
of the oviducts of the female are present in the form of short cœlomic
funnels opening into the kidney-ducts. It is probable that the other
male Ganoids also resemble Lepidosteus in the structure of their
urinogenital organs, which, however, require further investigation.

In the **Dipnoi** (Fig. 288) the elongated gonads are invested
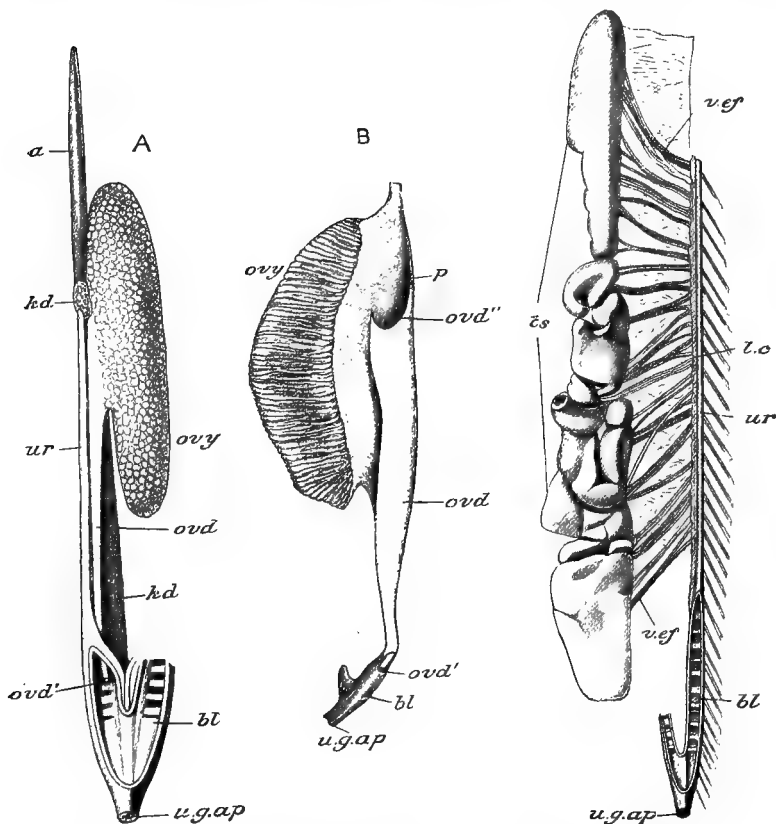


FIG. 286.

FIG. 287.

FIG. 286.—FEMALE URINOGENITAL ORGANS OF A, LEPIDOSTEUS, AND B, AMIA.
(A, after Balfour and Parker ; B, after Huxley.)

*a*, degenerate anterior portion of kidney ; *bl*, bladder ; *kd*, kidney ; *ovd*, oviduct ;
*ovd'*, aperture of oviduct into bladder ; *ovd''*, peritoneal aperture ; *ovy*, ovary ;
*p*, peritoneum ; *u.g. ap*, urinogenital aperture ; *ur*, kidney duct.

FIG. 287.—MALE URINOGENITAL ORGANS OF LEPIDOSTEUS. (After Balfour and
Parker.)

*bl*, bladder ; *l.c*, longitudinal canal ; *ts*, testis ; *u.g, ap*, urinogenital aperture ; *ur*,
kidney duct ; *v.ef*, vasa efferentia.
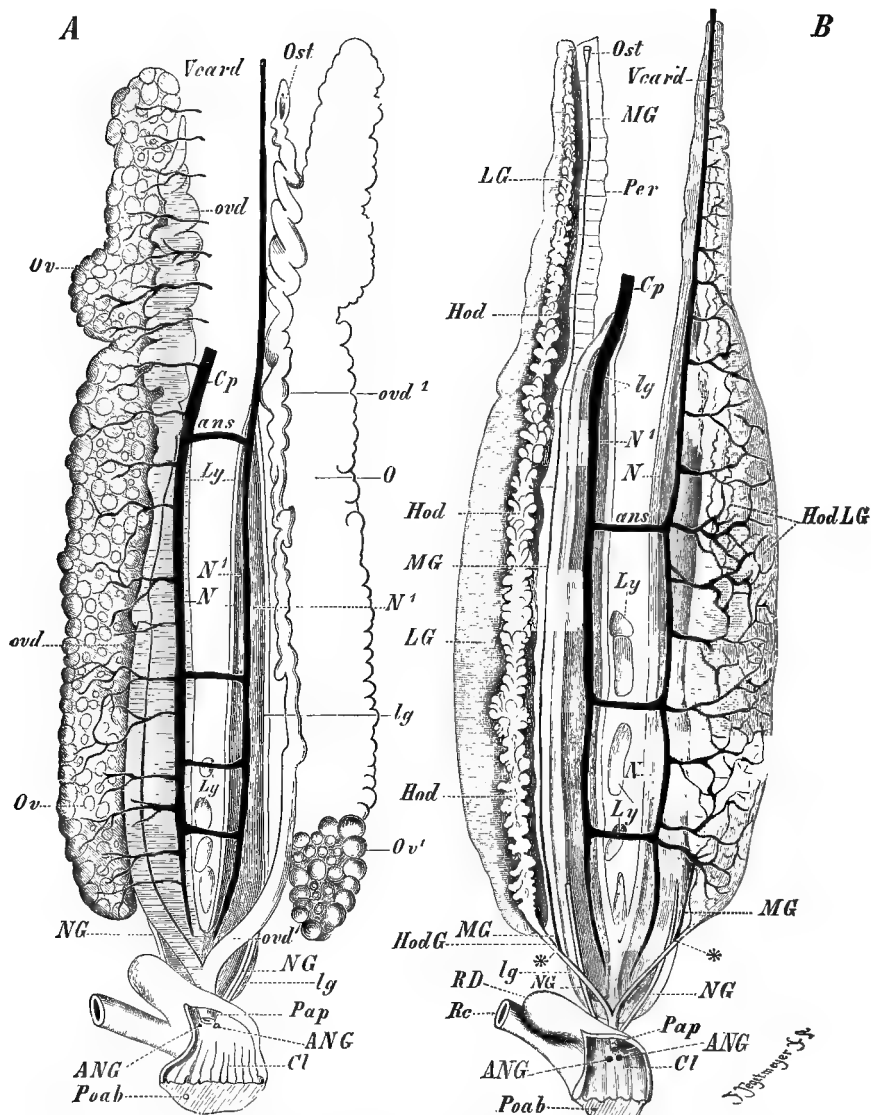
FIG. 288.—URINOGENITAL ORGANS OF *Protopterus annectens.* A, FEMALE; B, YOUNG MALE. From the ventral side. (After W. N. Parker.) The peritoneum is removed on the right side in A, and on the left in B.

*In both figures :* N,N¹, kidneys ; *Ost,* cœlomic aperture of Müllerian duct ; *ly, lg,* lymphatic tissue in connection with the kidneys ; *NG,* kidney ducts ; *ANG,* apertures of kidney ducts into the cloaca (*Cl*) ; *Pap,* genital papilla in the cloaca formed by the fusion of the base of the Müllerian ducts ; *RD,* cloacal cæcum ; *Rc,* rectum ; *Poab,* abdominal pore ; *Cp,* postcaval vein, connected by transverse anastomoses (*ans*) with the left posterior cardinal vein (*V.card*). The veins from the gonads are also indicated.

*In A .* OV, Ov¹, ovaries ; *ovd, ovd',* oviducts.

*In B :* *Hod,* testes, with their investment of lymphoid and adipose tissue (*LG*) ; *Hod.G,* free portion of sperm-duct, uniting with the Müllerian duct (*MG*) at *. Per, peritoneum.

with lymphoid and adipose tissue, and are closely attached to the outer border of the kidneys ; when ripe, they become greatly enlarged, so as to embrace the gut ventrally. The oviducts, which doubtless correspond to Müllerian ducts, are long and coiled, resembling those of the Amphibia: posteriorly they unite before opening into the cloaca, and each communicates anteriorly with the body-cavity by a funnel-shaped aperture. The wall of the oviduct secretes albumen round the eggs as they pass along it.

The manner in which the sperm is conducted to the exterior in Ceratodus is not understood. In Protopterus (Fig. 288, B) the seminal tubules of the testis open into a duct, embedded between the lobes of the testis ventrally. Behind the testis the duct extends freely for a short distance, and then unites with the base of the Müllerian duct, which, as in the female, joins with its fellow to open into the cloaca on the summit of a papilla. The rest of the Müllerian ducts, with their ostia, can still be recognised in immature individuals. The sperm-duct of Protopterus is apparently a structure *sui generis* ; like that of Teleosts, it is probably developed quite independently of the nephridial system.

In the greater number of **Elasmobranchs** the ovaries are paired, and the oviducts, like those of Dipnoans, are separate from the ovaries, and correspond to Müllerian ducts. Their anterior portion has a common opening into the body-cavity, and further back each is provided with an oviducal or shell-gland. The anterior part of the oviduct is always narrower and more delicate than the posterior, which dilates to form a kind of *uterus*, in which (when the Shark is viviparous) the embryo undergoes development. Posteriorly, the oviducts open into the cloaca somewhat behind the aperture of the ureters—either separately, or by a common canal (Figs. 278, B, 289).

The oviducal gland secretes the horny material for the egg-case or "purse," which is usually elongated and produced at its four angles into longer or shorter tendril-like threads ; in Cestracion it has a spiral ridge. The majority of Sharks are viviparous, and in these the egg-shell becomes more or less reduced. In Mustelus antarcticus the uterus becomes divided into several compartments, each containing an embryo surrounded by a membrane apparently representing the horny egg-shell of other forms.

The testis of Elasmobranchs is paired and symmetrical, but the two organs may become partially fused with one another. Vasa efferentia connect each testis with the anterior end of the corresponding mesonephros (parorchis), the Wolffian duct serving as a vas deferens (p. 346), and giving rise to a dilated portion or vesicula seminalis, as well as to a cæcal sperm-sac where it communicates with the urinogenital sinus : the latter opens into the cloaca on the apex of a papilla (Figs. 206, 278, C, 290). Vestiges of the anterior end of the Müllerian ducts can be recognised even in the adult as a short transverse tube with a central aperture, situated below the œsophagus anteriorly to the liver.

Fertilisation is internal in all Elasmobranchs except Læmargus, in which generative ducts are said to be wanting.
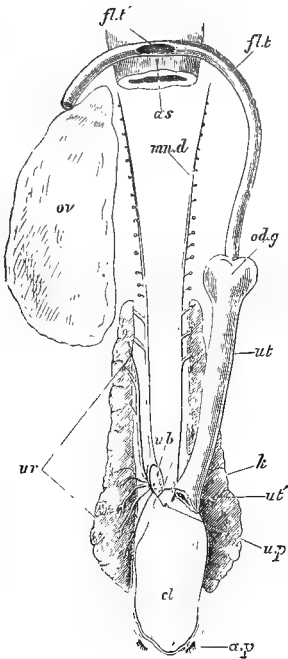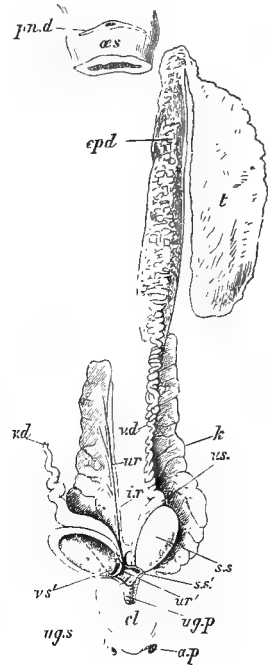


FIG. 289.　　　　　　　　　FIG. 290.

FIGS. 289 and 290.—FEMALE AND MALE URINOGENITAL ORGANS OF *Raja batis*. × ⅓.
(From T. J. Parker's *Zootomy*.)

*a.p*, abdominal pore ; *cl*, cloaca ; *epd*, left epididymis (the right is removed); *fl.t*, anterior portion of oviducts (Müllerian duct); *fl.t'*, common opening of the two oviducts into the cœlome ; *i.r*, internal body ; *k*, kidney ; *mn.d*, mesonephric (Wolffian) duct ; *od.g*, oviducal gland ; *œs*, œsophagus ; *ov*, right ovary (the left is removed); *pn.d*, remains of anterior part of Müllerian duct ; *s.s*, sperm sac ; *s.s'*, its opening into the urinogenital inus ; *t*, left testis (the right is removed); *u.b*, dilated end of mesonephric duct ; *ug.p*, urinogenital papilla ; *ug.s.*, urinogenital sinus ; *u.p*, urinary papilla ; *ur*, kidney ducts ; *ur'*, opening of kidney duct into the urinogenital sinus ; *ut*, uterine portion of left oviduct (that on the right side is removed) ; *ut'*, its opening into the cloaca ; *v.d*, vas deferens ; *v.s*, vesicula seminalis ; *v.s'*, its opening into the sperm-sac.

In female **Holocephali** the generative organs are essentially similar to those of Elasmobranchs, but in the male they present certain peculiarities. The unripe sperms pass into the immense epididymis, in which they become ripe and invested by spermato-

phores, which pass into a large vesicula seminalis at the base of the vas deferens; the Müllerian ducts are complete in the male, though small.

*Hermaphroditism* occurs amongst Fishes. In Myxine the posterior part of the gonad usually first gives rise to spermatozoa, and subsequently the anterior part to ova, so that self-fertilisation is prevented. Serranus and Chrysophrys, again, are hermaphrodite, and hermaphroditism has been occasionally observed in various other Fishes (*e.g.*, Gadus morrhua, Scomber scomber, Clupea, Harengus).

**Amphibia.**—The paired and symmetrical gonads of Amphibians are situated in about the middle of the cœlome; their form is usually modified by the shape of the body. Thus in the Gymnophiona the ovary has the form of a long and narrow band, while the testis is made up of a long chain of small bodies united together by a collecting duct (Fig. 291). Each individual portion
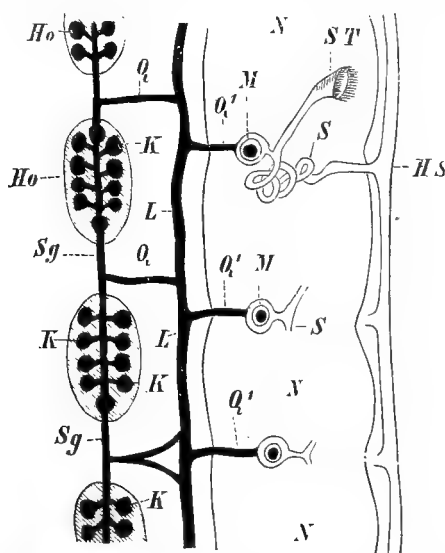


FIG. 291.—DIAGRAM OF A PORTION OF THE MALE GENERATIVE APPARATUS OF THE GYMNOPHIONA.

*Ho, Ho,* testis; *Sg,* collecting duct of testis; *K, K,* testicular capsules; *Q, Q* transverse canals connecting the collecting duct with the longitudinal canal (*L, L*); *Q¹, Q¹,* second series of transverse canals; *M, M,* Malpighian capsules; *N, N,* kidney; *ST,* nephrostome; *S,* convoluted portion of urinary tubule; *HS,* urinogenital duct.

of the testis of Cæcilians is made up of a double row of rounded capsules in which the sperm is formed, and from which it is passed into a collecting duct, which perforates each portion of the organ. A transverse canal is given off from the free portion of the collecting duct lying between every pair of testis lobes; this passes to-

wards the kidneys, and opens into a longitudinal canal.   From the
latter the sperm passes through a second system of transverse canals
to the Malpighian capsules, and thence through the urinary tubules
into the urinogenital duct.

The male generative apparatus of all Urodela and certain
Anura (comp. p. 354) corresponds in the main with that seen in
Cæcilians, except as regards the form of the gonads : thus the testis
is either pointed at one or both ends (Fig. 279), or more or less
round or oval (Figs. 280, 292).

In Rana, Bombinator, and Alytes the vasa efferentia of the testis become
gradually separated from the kidney : that is, they either open directly into
the urinogenital duct, without becoming connected with the urinary tubules
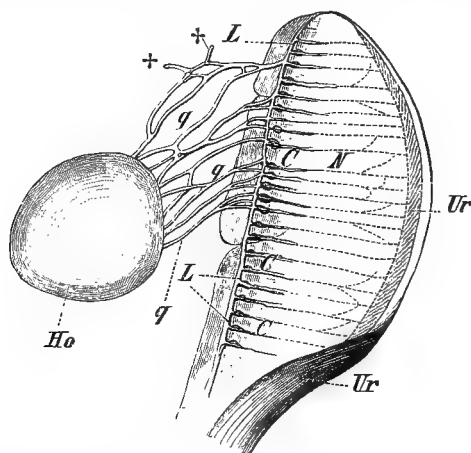


FIG. 292.—TESTIS AND ANTERIOR END OF KIDNEY OF *Rana esculenta.*
(Semidiagrammatic.)

*Ho*, testis ; *q, q*, transverse canals of the testicular network, which give rise to
   blind processes at † † ; *L*, longitudinal canal of the testicular network, from
   which the interrenal network (*C, C*) arises ; *N*, kidney ; *Ur*, urinogenital
   duct.

(Rana, Fig. 292), or the greater number of the posterior canals end
blindly, while only the anterior ones are directly connected with the
urinogenital duct (Bombinator).   In Alytes the relations of the generative
ducts require further investigation.

Müllerian ducts are always present, but they always remain in a more or
less rudimentary condition in the male, and lie along the outer border of the
kidneys in a similar position to those of the female.   They may or may not
be provided with a lumen and apertures of communication with the body-
cavity and cloaca.

*Hermaphroditism* occasionally occurs amongst the Anura : only one case
(Triton tæniatus) is known amongst Urodeles.   A body attached to the
anterior end of the testis in various species of Toads ("Bidder's organ") is
apparently capable of giving rise to ova and spermatozoa.   In the males of
Rana temporaria ova are at times developed, embedded within the sub-

stance of the testis (*hermaphrodite gland* or *ovotestis*), and one testis may even be replaced by a rudimentary ovary. In these cases, the Müllerian duct may be as well developed as in the female.

The ovaries of Urodela are always formed on a common plan : each consists of an elongated closed tube, with a continuous lumen. In Anura, on the contrary, the ovarian sac (Fig. 293) is divided up
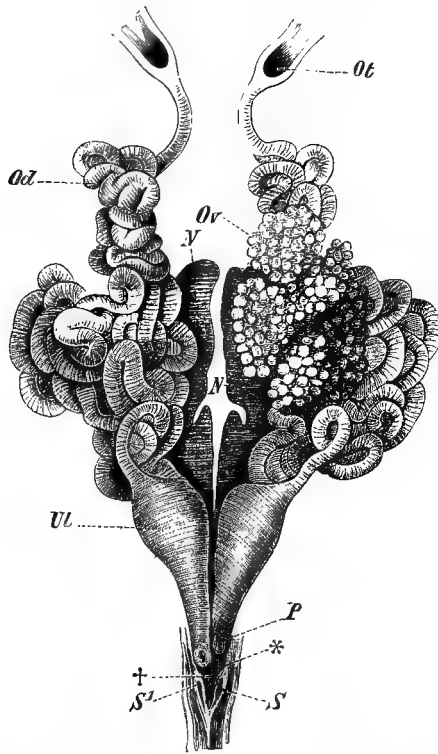


FIG. 293.—URINOGENITAL ORGANS OF A FEMALE *Rana esculenta.*

*Ov*, left ovary (that of the right side is removed); *Od*, oviduct; *Ot*, abdominal aperture of oviduct ; *Ut*, the dilated posterior end of the oviduct ; *P*, opening of latter into the cloaca ; *N*, kidneys ; *S*, *S¹*, apertures of urinary ducts into the cloaca, surrounded by longitudinal folds (*), which are separated by a deep depression (†).

into a longitudinal row of numerous (3 to 20) separate pockets or chambers. The oviducts open far forwards into the body-cavity by funnel-shaped apertures; they take a tolerably straight course along the outer borders of the kidneys to the cloaca in young animals, but become greatly convoluted later. A short distance from its termination each oviduct in Anurans becomes dilated to form a thin-walled sac, and, after becoming again narrowed, usually

opens separately on a papilla on the dorsal wall of the cloaca. Only in the genera Bufo and Alytes do the two oviducts fuse together into a posterior unpaired canal.

In female Urodeles a number of tubes serving as a receptaculum seminis may be present in connection with the cloaca, and the male is provided with a cloacal gland which secretes spermatophores.

After receiving a gelatinous coating from the glands in the wall of the middle part of the oviduct, the eggs of Anurans pass into the dilated portion of the duct, and become united together into irregular masses (Frog) or chains (Toad).

In Epicrium glutinosum (Gymnophiona) the eggs are very similar to those of Sauropsida : they are exceptionally large (9 mm. long), of an oval shape, and possess a large yolk. They become coated after fertilisation with a tough albumen in the oviduct, and this becomes drawn out at the poles into chalazæ, by means of which the eggs are connected together like the beads of a necklace. The segmentation is *meroblastic*, and takes place in the oviduct ; and the eggs are laid in the earth, the mother coiling herself round them.

Fat-bodies (*corpora adiposa*) are present in all Amphibia in connection with the gonads : they are formed of adenoid substance, fat, and leucocytes, and contain numerous blood-vessels.

The corpora adiposa probably have an important physiological (nutritive) relation to the gonads : Amphibians, after remaining for months without food, throughout their winter sleep, are able as soon as spring arrives to give rise to thousands of offspring.

**Reptiles and Birds.**—The essential differences between the urinogenital organs of the Anamnia and Amniota have already been described (pp. 346, 356, and Fig. 273).

In the Sauropsida, as in other Vertebrates, the form of the gonads is influenced by that of the body : thus in Chelonians they are broad, while in Snakes and snake-like Lizards they are more elongated. In the latter cases, as well as in other Lizards, they are asymmetrical, so that the organ of one side is situated more or less in front of that of the other. More room is thus obtained for the development of the ovaries; and, in cases where the eggs are very large, the organ of one side tends to disappear, as in certain Elasmobranchs (*e.g.*, Scyllium) : in Birds, for instance, the left ovary only is completely developed and functional.

In Reptiles the ovaries are penetrated by a highly vascular network of trabeculæ, and in the lymph-cavities thus formed the formation of ovarian follicles takes place.

The oviducts (Fig. 294) possess wide funnel-shaped abdominal apertures, and are usually much folded transversely ; the right is often longer than the left. Their walls are provided with numerous muscular elements and glands for the formation of the albumen and egg-shell, and they increase in size in the breeding-season. In Birds the right oviduct, as well as the right ovary, becomes more or less completely degenerated ; the left oviduct is considerably coiled.

Only slight remnants of the mesonephros and Wolffian duct persist in female Reptiles, and these undergo fatty degeneration. They are asymmetrical, and are arranged in a single row on either side, between the oviduct
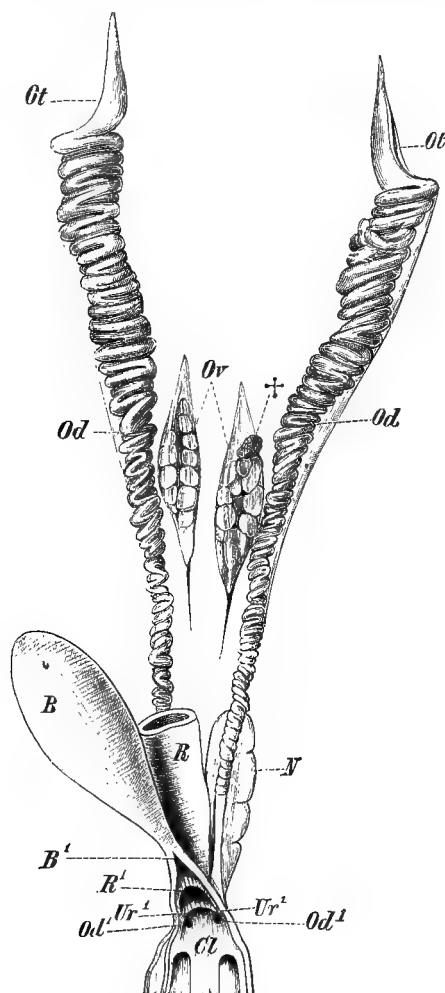


FIG. 294.—FEMALE URINOGENITAL APPARATUS OF *Lacerta muralis.*

*N*, kidneys; *Ur*[1], apertures of the ureters into the cloaca (*Cl*); *B*, urinary bladder; *B*[1], neck of the latter (cut open); *R*, rectum; *R*[1], opening of rectum into the cloaca; *Ov*, ovaries; †, remains of mesonephros; *Od*, oviducts, which open into the cloaca at *Od*[1]; *Ot*, abdominal openings of oviducts.

and vertebral column. The remains of the Wolffian duct are more marked in female Snakes, Chelonians, and in Geckos than in the majority of Lizards.

The testes of Sauropsida correspond in position with the ovaries, and, like them, increase in size in the breeding-season. They have an oval, round, or pyriform shape (Figs. 283 and 295), and are made up of greatly convoluted seminal tubules, held together by fibrous tissue. In Reptiles (*e.g.* Lacerta, Anguis), "yellow bodies," which correspond to suprarenals (p. 385), lie along the outer border of the testis, and at this point transverse canals pass out from the testis to the parorchis.
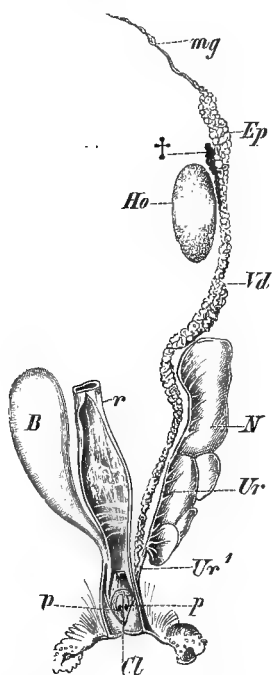
The latter consists of greatly convoluted canals, and from it arises the vas deferens (Wolffian duct), which either takes a straight course, or is more or less coiled. In Birds it opens by an independent aperture into the cloaca, while in Lizards it fuses with the ureter shortly before entering the latter.

Remains of the Müllerian ducts are present in the male, corresponding in position with those of the female. Their lumen is not continuous throughout, but the abdominal aperture may remain open (Emys europæa), and exceptionally (*e.g.* Lacerta viridis) they may be as well developed as in the female.

Lymphoid organs are present in many Reptiles, and probably have a physiological relation to the generative organs (compare p. 368). In many Lizards they are large and variously coloured, and lie within the pelvic region; in Snakes they extend along almost the entire body-cavity.

Hermaphroditism has been observed very exceptionally in the Chaffinch. Occasionally the ovary of some Birds undergoes structural changes, and no longer produces ova, the female then taking on certain secondary sexual characters of the male.



FIG. 295. —MALE URINOGENITAL ORGANS OF *Anguis fragilis.* (After F. Leydig.)

*Ho*, testis; †, the so-called "yellow body" (suprarenal); *Ep*, parorchis; *Vd*, vas deferens; *p*, *p*, common aperture of the ureter (*Ur*, *Ur*¹) and vas deferens on a papilla on the dorsal wall of the cloaca (*Cl*); *B*, urinary bladder; *r*, rectum; *N*, kidney; *mg*, rudiment of the Müllerian duct.

**Mammals.**—In Mammals the generative apparatus no longer extends along the entire body-cavity, as in the lower Vertebrates, but is confined to the lumbar and pelvic regions. Moreover, in correspondence with the close relations which usually take place between mother and embryo (p. 338), there is a much greater differentiation of the generative organs than occurs in lower types. The transition is not, however, a sudden one, for in the lowest Mammals, viz., the Montremes and Marsupials (Figs. 296 and 297),

these organs show many points of resemblance with those of Reptiles and Birds.
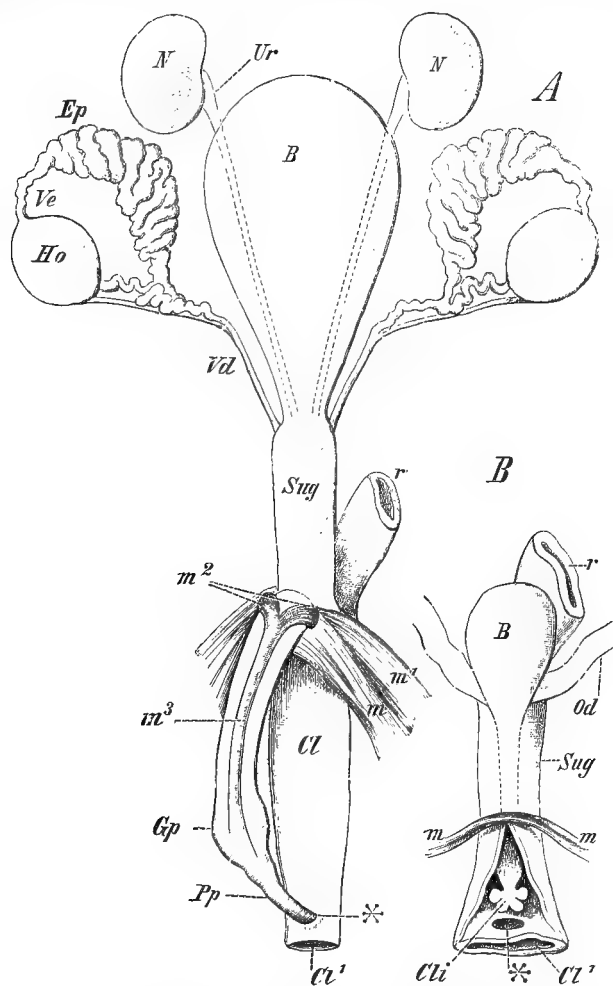


FIG. 296.—A, MALE URINOGENITAL ORGANS OF *Ornithorhynchus paradoxus*; B, FEMALE URINOGENITAL ORGANS OF *Echidna hystrix*.

*N*, kidneys; *Ur*, ureter; *B*, urinary bladder; *Sug*, urinogenital canal; *Ho*, testis; *Ve*, vas efferens; *Ep*, epididymis; *Vd*, vas deferens; *Od*, oviduct; *r*, rectum; *Cl*, cloaca, opening to the exterior at *Cl¹*; *m* to *m³*, muscles of the cloaca and penis (or clitoris); *Gp*, glans penis, enclosed within its fibrous tube; *Pp*, prepuce; *Cli*, clitoris; ✳, aperture through which the copulatory organ extends into the cloaca.

Thus in the oviparous Monotremes the left ovary is more strongly developed than the right, and each has the appearance of a bunch of grapes; the cloaca persists, and the oviducts (Müllerian ducts),
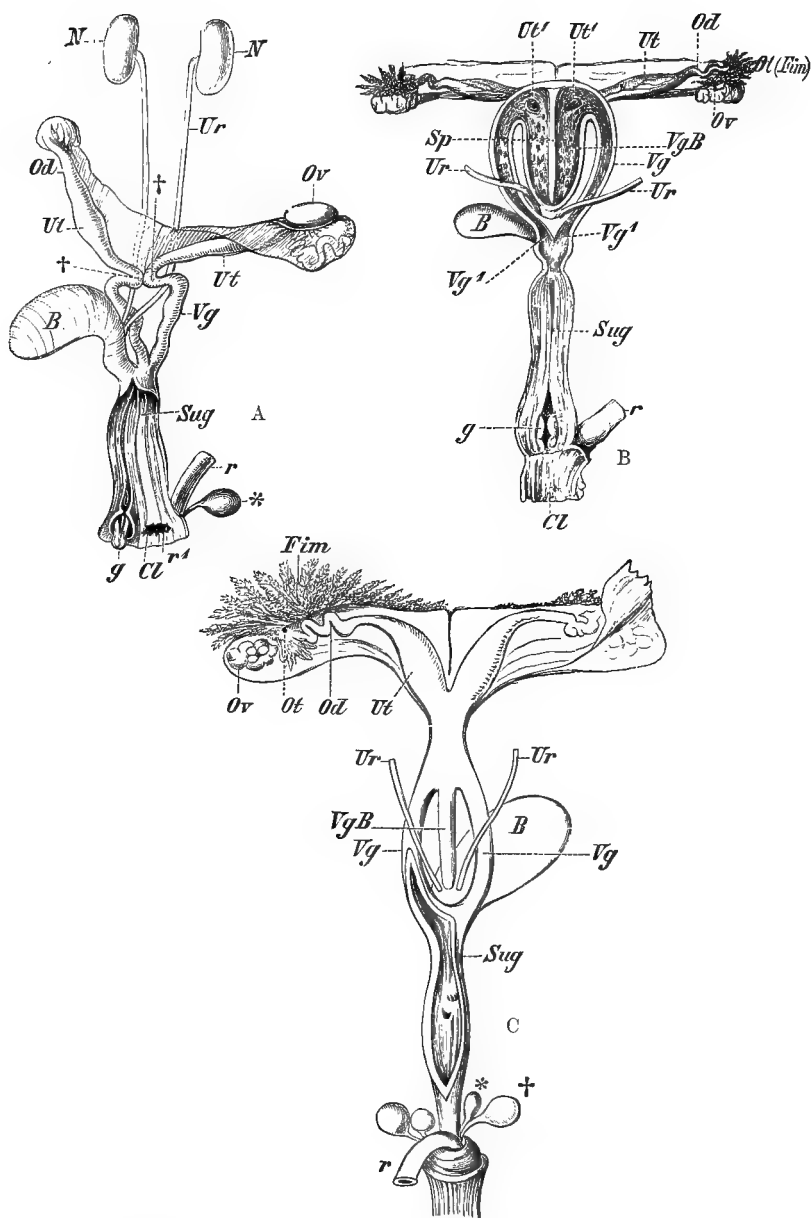
FIG. 297.—FEMALE GENERATIVE APPARATUS OF CERTAIN MARSUPIALS. A, *Didelphys dorsigera (juv.)* ; B, *Phalangista vulpina* ; C, *Phascolomys wombat.* (After A. Brass.)

*NN*, kidneys ; *Ur*, ureters ; *Or*, ovary ; *Ot (Fim)*, abdominal opening of Fallopian tube ; *Od*, oviduct ; *Ut*, uterus ; *Ut¹*, openings of uteri into the vaginal cæcum, *VgB* ; †, bend between uterus and vagina, *Vg* ; *Vg¹*, apertures of vaginæ into the urinogenital canal (*Sug*) ; *B*, urinary bladder ; *r*, rectum, which opens to the exterior (*Cl*) at *r¹* ; *g*, clitoris ; *, †, rectal glands.

which in other Mammals become more or less fused with one
another proximally, remain distinct throughout, and open into the
urinogenital canal anteriorly to the ureters and bladder.

In the higher Mammals the oviducts become distinctly differ-
entiated into three portions,—a *Fallopian tube*, a *uterus*, and a
*vagina*. The vagina opens to the exterior (Figs. 273, 297, 298),
while the Fallopian tube communicates with the abdominal cavity
by a ciliated funnel-shaped aperture.

In Marsupials the fusion of the two oviducts is much less
marked than in the higher Mammals, and in order to trace
the gradual differentiation of these parts, their condition in Opos-
sums (Didelphidæ) must now be described in greater detail.

A dilated portion of each oviduct (Fig. 297, A), giving rise to a
uterus, is plainly distinguishable from the rest, and its narrowed
posterior end comes into close contact with its fellow in the middle
line. At this point (†) each uterus communicates with the vagina
by a distinct *os uteri*. The vagina curves sharply outwards, and,
then backwards, opening close to its fellow into the elongated urino-
genital canal. The ureters, as in all other Marsupials in which the
vaginæ have a similar arrangement, pass between the curved
portions of the vaginæ to the bladder.

From the condition of the female generative organs in Didel-
phys, that seen in other Marsupials can be easily explained. In
Phalangista vulpina and Phascolomys wombat (Fig. 297, B and C)
the anterior ends of the knee-shaped bends of the vaginæ lie
closer together, and begin to extend backwards towards the urino-
genital canal, the septum between them disappearing at the
same time. A *vaginal cœcum* is thus formed : this may
become more elongated, and finally extend backwards so as to
meet the anterior wall of the urinogenital canal, into which it
may open by the formation of a so-called *third vagina*. The
anus and urinogenital apertures are surrounded by a common
sphincter.

In the placental Mammals the posterior portions of the Müller-
ian ducts become fused together to form an unpaired vagina, and a
definite cloaca exists only in the embryo, although even in the
adult in certain cases (*e.g.*, amongst Rodents), the anus and urino-
genital aperture may be enclosed by a common fold of the integu-
ment as in Marsupials, and a median septum may be present in
the vagina distally, indicating its primary double nature. The
uterine portions of the oviducts may also fuse with one another to
a greater or less extent, and thus the most various forms of uteri
result (*uterus duplex, bicornis, bipartitus,* and *simplex*), as shown in
Fig. 298, A to D. The Primates possess a single uterus, and in this
case the primitively paired condition of the Müllerian ducts is seen
only in the Fallopian tubes. The latter vary much in form, and
their abdominal apertures are usually provided with fringe-like
appendages (fimbriæ). The ureters, unlike those of Marsupials,
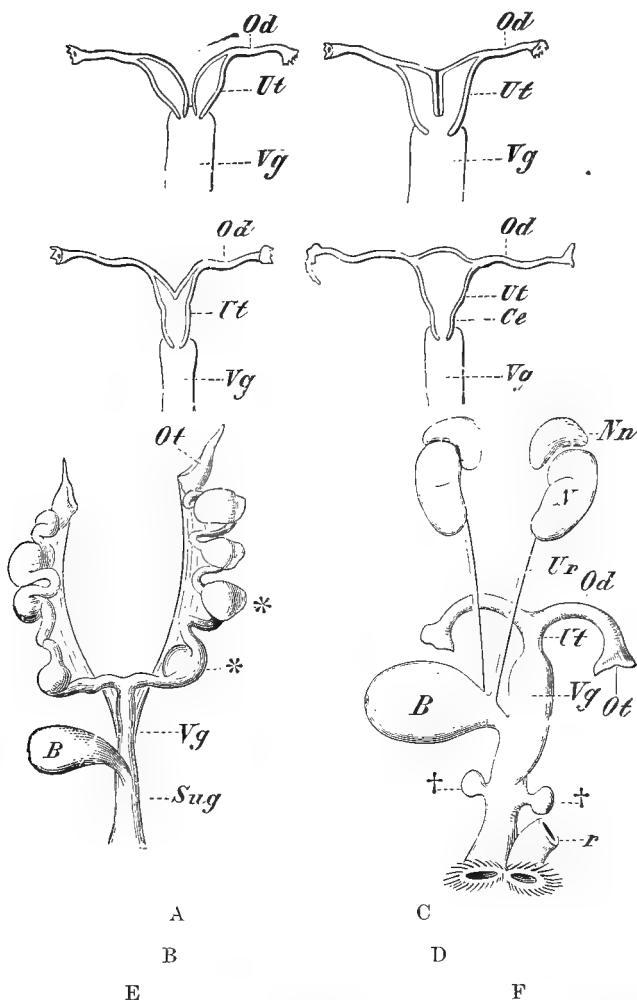
Fig. 298.—Various Forms of Uteri. A, B, C, D, diagrams showing the different stages in the fusion of the Müllerian ducts : A, uterus duplex ; B, uterus bicornis ; C, uterus bipartitus ; D, uterus simplex ; E, female urino-genital apparatus of *Mustelina*, containing embryos (*, *) in the uterus ; F, ditto of Hedgehog (*Erinaceus*).

*Od*, Fallopian tube ; *Ut*, uterus ; *Vg*, vagina ; *Ce*, cervix uteri ; *Ot*, abdominal aperture of Fallopian tube ; †, †, accessory glands ; *r*, rectum ; *Sug*, urino-genital canal ; *K*, kidney ; *Nn*, adrenal ; *Ur*, ureter ; *B*, urinary bladder.

always pass to the outer sides of the genital passage, the vagina being single.

The urinogenital canal may, as in Marsupials, be of a consider-able length (*e.g.* amongst Rodents), and a fold of the mucous

membrane (*hymen*)[1] is often present where the vagina opens into it.   On the ventral (anterior) wall of the urinogenital canal, the *clitoris* (Pp. 380–384) is situated.   In both male and female the space between the urinogenital aperture and the anus is known as the *perinæum*.

The ovaries are usually small, and rounded or oval in shape, their surface being either smooth, irregular, or furrowed. The point at which the nerves and vessels enter is not covered by peritoneum, and is called the *hilum*.

Remains of the mesonephros, known as the *parovarium*, are present in the neighbourhood of the ovary, oviduct, and uterus.   These usually consist of small cæcal tubes, forming a network, which are connected together by a collecting duct.   In cases where the Wolffian duct persists in the female, it passes from the parovarium to the urinogenital sinus and is spoken of as *Gartner's duct* (Fig. 273, H).

A fold of the skin of the abdomen forming a *pouch* or *marsupium* is present in Echidna and to a greater or less extent in Marsupials (p. 28): this serves to protect the egg (Echidna) and young, which in the latter are born in a very unripe condition, thus rendering possible a longer connection between the mother and embryo during lactation.   The aperture of the marsupial pouch opens anteriorly or posteriorly, according to the mode of life of the animal, and is provided with a muscle capable of closing it.   In Marsupial embryos the margins of the lips become partially fused secondarily and temporarily to form a suctorial mouth, by means of which the young, many of the organs of which are still in a "larval" condition, become attached to the teats (compare p. 288).

In male Mammals, the testes arise in the same relative position as the ovaries of the female.   The ovary, however, never moves in the course of development further backwards than the pelvis ; but the testis may pass out of the abdomen through an *inguinal canal* into a purse-like outgrowth of the integument in the inguinal region called the *scrotal sac*, which is lined by a continuation of the peritoneum, the *tunica vaginalis*.   The two scrotal sacs (which are represented amongst female Primates by the so-called labia majora of the vulva) may remain separate, or unite to form a *scrotum* : in Marsupials this is situated in front of, and in placental Mammals behind the penis (p. 382).   If the inguinal canals remain widely open, they may be withdrawn periodically into the abdomen (as *e.g* in Rodentia and Insectivora, in which they only descend at sexual maturity) ; this is effected by means of the *cremaster muscle*, a continuation of the fibres of the internal oblique and transversalis, or of the latter only, and corresponding to the "compressor mammæ" of Marsupials.   When the inguinal canals become reduced, the testes remain throughout life in the scrotum.   In many Mammals, how-

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[1] A similar fold, closing the apertures of the oviducts in the immature condition, is present in Elasmobranchs.

ever (*e.g.*, Monotremes, most Edentates, Elephant), the testes remain permanently within the abdomen.

The testes are smooth, and somewhat oval in form, and their relative size varies in different Mammals; they are covered by a
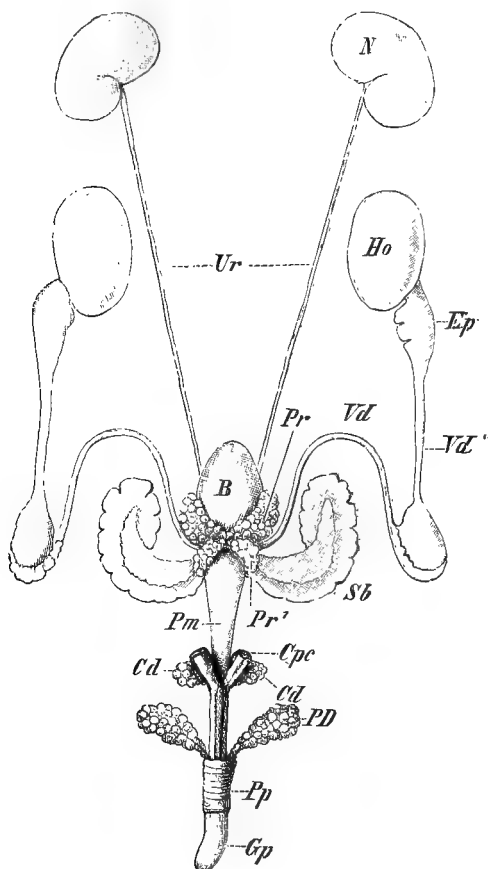


FIG. 299.—MALE URINOGENITAL APPARATUS OF THE HEDGEHOG (*Erinaceus*).

*N*, kidney; *Ur*, ureters; *B*, urinary bladder; *Pm*, membranous portion of urinogenital tube; *Cpc*, corpus cavernosum; *Pp*, prepuce; *Gp*, glans penis; *PD*, preputial glands; *Cd*, Cowper's glands; *Pr*, *Pr*[1], the different lobes of the prostate; *Sb*, vesicula seminalis; *Ho*, testis; *Ep*, epididymis; *Vd*, *Vd*[1], vas deferens.

fibrous investment (Fig. 300), from which processes (trabeculæ) usually extend inwards. Thus the seminal tubules become separated into definite lobed masses, and a sort of lattice-work is also formed (corpus Highmori), through which the elements of the vasa efferentia pass to the *epididymis*. In the latter the

seminal tubules become rounded off to form the so-called *coni vasculosi*, and these are connected together by a collecting duct, the *vas epididymitis*.    The vas deferens arises from the last conus vasculosus, and gives rise towards its distal end, shortly before it opens into the urinogenital sinus close to an elevation—the colliculus seminalis, to glandular outgrowths (*vesiculæ seminales*), which may attain a relatively enormous size in Rodents and Insectivores (Fig. 299).    From this point to its termination at the
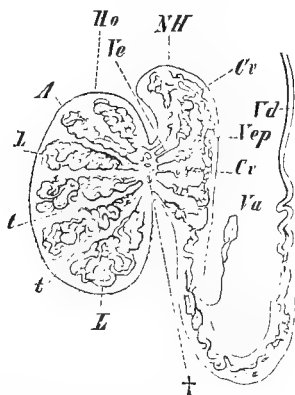


FIG. 300.—DIAGRAMMATIC SECTION OF THE TESTIS OF A MAMMAL.

*Ho*, testis ; *NH*, epididymis ; *Vd*, vas deferens ; *A*, albuginea of the testis, which gives rise to the trabeculæ (*t, t*) and the corpus Highmori (†) ; *L, L*, coils of the seminal tubules ; *Ve*, vasa efferentia (rete Halleri) ; *Cv*, coni vasculosi, which are connected together by the collecting duct, *Vep* ; *Va*, vas aberrans.

apex of the penis, the seminal canal is spoken of as the *ductus ejaculatorius*.

In many Mammals rudiments of the Müllerian ducts are present in the male, and open into the urinogenital sinus.    In Man, only the most posterior end of the ducts remain in the form of an unpaired vesicle (*uterus masculinus*), which lies embedded within an accessory genital gland, the *prostate* (Fig. 299).    This gland, which more or less completely surrounds the urinogenital sinus, consists of glandular tubules connected together by means of fibrous and muscular tissue : its secretion is poured into the urinogenital sinus, and is apparently of great importance in connection with the activity of the spermatozoa.

### Copulatory Organs.

Various forms of copulatory organs, morphologically distinct from one another, occur amongst Vertebrates.    In male **Elasmobranchs** a specially modified portion of each pelvic fin (*clasper* or *pterygopodium*, p. 122) serves this purpose.    It consists of a series

of more or less calcified cartilages, covered by skin and muscles, which are movable upon one another and are derivatives of the fin-rays, and it is provided with a channel along the inner side. These claspers are inserted, in a closed condition, into the cloaca of the female, and thence into the oviducts ; they are then opened out by means of special muscles, and the seminal fluid flows along their channels into the distended oviducts. In connection with this apparatus there is a gland (p. 18) surrounded by muscular fibres, which is formed as an involution of the integument; in its histological character this calls to mind the uropygial gland of Birds (p. 21).

In addition to pterygopodia, similar to those of Elasmobranchs the **Holocephali** possess a pair of curious *anterior claspers* (Fig. 301), which are protruded from a shallow pouch situated
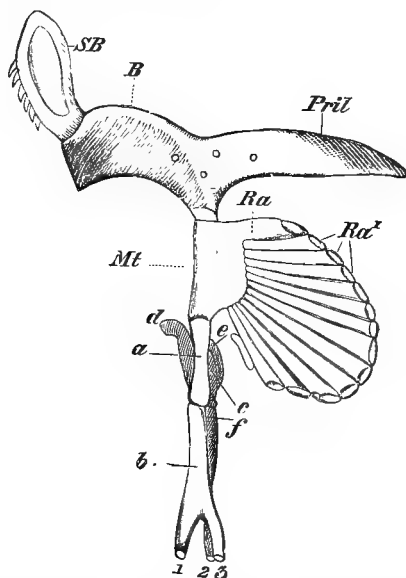


FIG. 301.—PELVIC ARCH AND SKELETON OF PELVIC FIN AND CLASPER OF A MALE *Chimaera monstrosa*. (After Davidoff.) Ventral view.

*Pr.il*, *B*, dorsal part of pelvic arch (iliac process) ; *S.B*, anterior clasper ; *a—f*, 1—3, the various segments of the posterior clasper ; *Mt*, basipterygium ; *Ra*, *Ra¹*, radii of fin.

in front of the pelvic fins ; each of these consists of a plate covered with dermal denticles, and in Callorhynchus a grooved structure is present in addition.[1] There is also a knob-like organ, usually known as the *frontal clasper*, on the upper surface of the head. (Fig. 57).

[1] These may correspond to portions of the primitive lateral fin-folds (p. 103) which are not represented in other Craniata.

Amongst the **Teleostei**, the terminal portion of the anal fin in the male Girardinus is modified to form an apparatus for holding the female, and in many Cyprinoids certain modifications occurring in the anal fin may have a similar function.

Amongst the **Amphibia,** a marked swelling of the lips of the cloaca may occur in Urodeles during the breeding season and internal impregnation may take place, but only in the male Gymnophiona is a definite copulatory organ present ; this simply consists of the eversible cloaca, which is regulated by a well-developed musculature (Fig. 302).
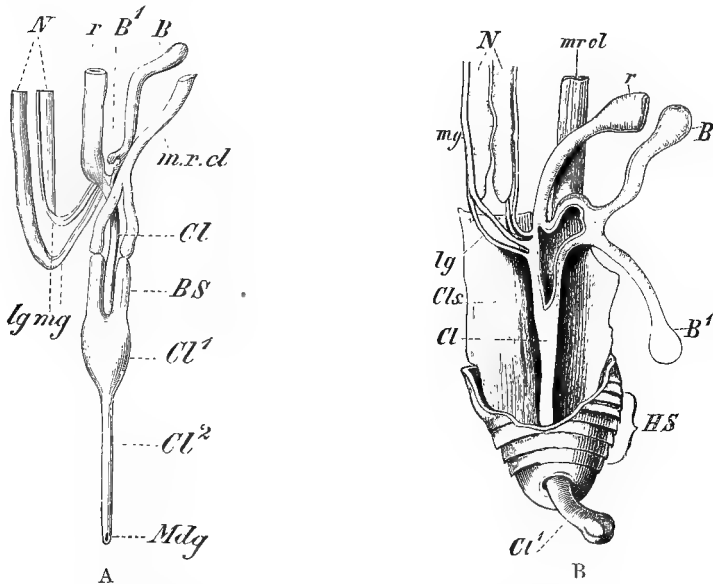


Fig. 302.—The Posterior Part of the Urinogenital Apparatus of A, *Epicrium glutinosum* and B, *Cæcilia lumbricoides.*

*Cl, Cl*[1], *Cl*[2], the different sections of the cloaca, and *Bs,* its cæcal processes : the cloaca is shown retracted in A and everted in B ; *cls,* cloacal sheath ; *m.r.cl,* retractor muscle of the cloaca ; *B, B*[1], the two horns of the urinary bladder ; *N,* kidneys ; *lg,* Wolffian duct ; *mg,* Müllerian duct ; *r,* rectum ; *Mdg,* cloacal aperture ; *HS,* scales in the integument.

Two kinds of copulatory organs are found in **Reptiles,** the one being seen in Lizards and Snakes, and the other in Chelonians and Crocodiles.

In the former there are two copulatory sacs or *penes* lying outside the cloaca, under the skin at the root of the tail, and these can be everted and protruded through the vent and again withdrawn by means of a muscle inserted into the blind end of the sac (Fig. 303). In its everted condition, a spiral furrow extends along each sac down

which the seminal fluid passes. These organs are also represented in the female, in which they are, however, much smaller.

In Chelonians and Crocodiles the penis is single, and corresponds to a thickened portion of the ventral wall of the cloaca
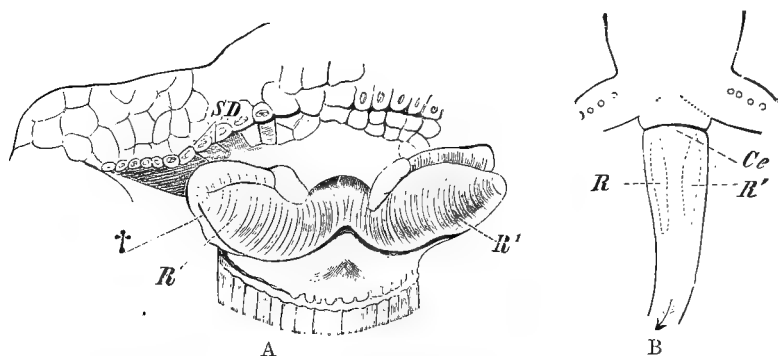


FIG. 303.—COPULATORY ORGANS OF *Lacerta agilis*. (After F. Leydig.) In A they are shown everted, and in B their position in the retracted condition is indicated by dotted lines extending backwards from the vent (*Ce*).

*R*, Penes ; †, spinal furrow ; *SD*, the so-called " femoral glands " (see p. 20).

(Figs. 304, 305, A). It consists of fibrous and cavernous (erectile) tissue, and is protrusible, being regulated by muscles. In the female it is represented by a smaller *clitoris*. The penis bifurcates
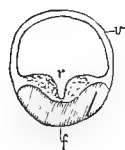


FIG. 304.—TRANSVERSE SECTION OF THE CLOACA OF A CHELONIAN. (Slightly diagrammatic.) After Boas.

*f*, fibrous body ; *r*, seminal furrow, bounded by cavernous tissue ; *c*, wall of cloaca.

proximally, and its distal tongue-shaped portion ends freely ; a longitudinal groove extends along the upper surface, at the proximal end of which the vasa deferentia open. In Crocodiles the free portion is relatively longer and the groove deeper than in Chelonians.

In many **Birds** a copulatory organ is present, formed on a similar plan to that of Chelonians and Crocodiles. It is well developed amongst the Ratitæ and Lamellirostres, and in many other Birds can be recognised in a rudimentary condition. In Struthio it resembles that of the Crocodile, and is supported by a
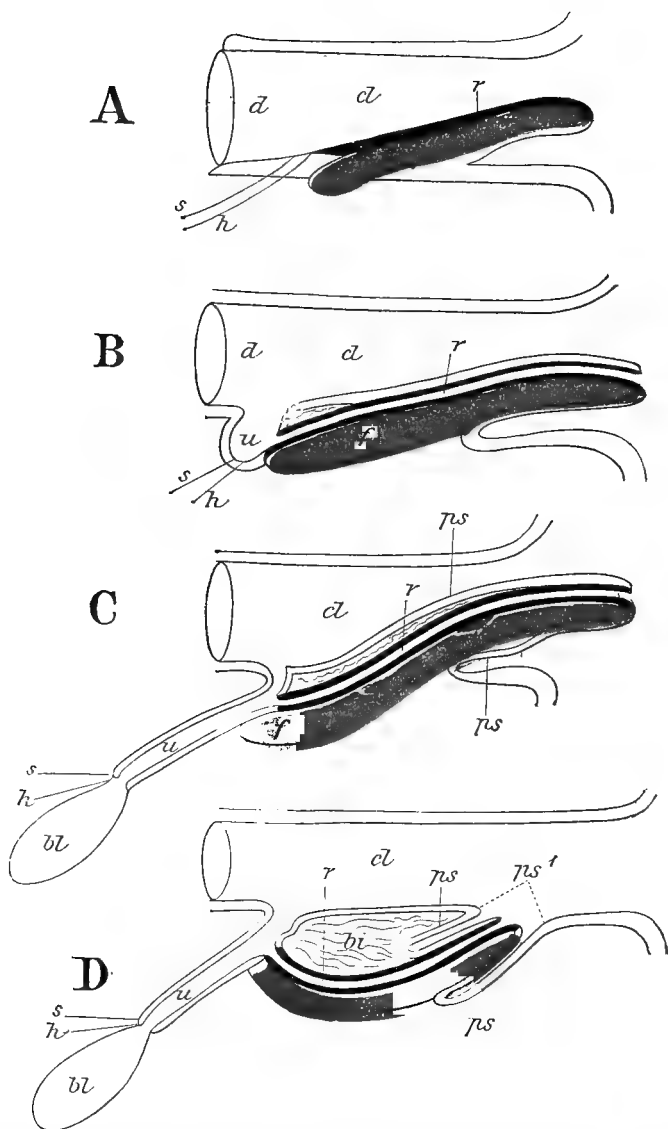
FIG. 305. DIAGRAMMATIC LONGITUDINAL SECTIONS OF THE POSTERIOR PART OF
THE RECTUM, THE CLOACA, AND THE COPULATORY ORGANS OF VARIOUS
VERTEBRATES. (After Boas.) The position of the ureter and vas deferens
are indicated, although not situated in the median line.

A, *Crocodile*; B, hypothetical form between A and C; C, *Monotreme* (penis
extruded); D, Monotreme (penis retracted).

*bi*, connective-tissue; *bl*, urinary bladder; *cl*, cloaca; *d*, rectum; *f*, fibrous body
(corpora cavernosa of human anatomy); *ps*, sheath of penis; *ps¹*, aperture of
the sheath; *r*, seminal furrow or tube (penial urethra); *s*, vas deferens; *u*,
urinogenital canal.

fibrous body, bifurcated at the base. In Dromæus and Rhea there is an aperture at the apex of the penis leading into an elongated and curved blind sac, in which is a furrow, lined by cavernous tissue, continuous with the groove on the dorsal side of the organ. In the Duck and Swan the spiral penis is essentially similar to that of Dromæus and Rhea. The absence of the blind sac in the Ostrich, however, is probably a secondary modification. A clitoris is present in the female of the above-mentioned Birds.

The penis of **Monotremes** may be best understood by imagining a hypothetical form intermediate between it and that of Crocodiles and Chelonians (Fig. 305, B). We must suppose that a sac-like outgrowth into which the ureter and vasa deferentia open has become developed from the ventral cloacal wall at the base (anterior end) of the penis, the groove in which has become converted into a canal. The Monotreme condition is reached by the sac elongating to form a urinogenital canal, into the distal end of which the urinary and genital ducts and the bladder open (C, D). The penis consists of an unpaired fibrous body enclosing the canal, and is only loosely surrounded by the mucous membrane of the cloaca, so that it can be protruded from and retracted into a sheath in which the apex or *glans* lies.

In Echidna, cavernous tissue is present in the glans; and in Ornithorhynchus the latter is bifurcated and covered with soft spines, the seminal canal opening in a groove on each fork by numerous fine canals situated on papillæ.

A clitoris is present in the female of all Mammals.

In **Marsupials** (Fig. 306, A), the penis-sheath opens directly on to the surface of the body; the opening of the urinogenital canal into the cloaca has become closed, and is continuous with the seminal tube or urethra of the penis. The fibrous body is paired, and both it and the walls of the penial urethra are composed of cavernous tissue.

Amongst **Placental Mammals** the penis of Rodents (Fig. 306, B) and Insectivores comes nearest to that of Marsupials. The paired fibrous body (*corpus cavernosum*) bifurcates proximally to form two crura, which are nearly always attached to the ischia. The opening of the penis-sheath gradually becomes further separated from the anus, and is situated more on the ventral side of the body (compare B and C), the penis itself lying horizontally along the abdomen. In Primates the organ becomes more or less free from the body-wall, and either its distal end (Apes, C), or the whole of it (Man, D) hangs freely, and the sheath forms a double tube-like investment, the foreskin or prepuce, over the glans.

In the course of development, the penis of Marsupials and Placental Mammals passes through stages which resemble successively those which are permanent in Crocodiles and Chelonians and in Monotremes. It arises from a " genital prominence " on the
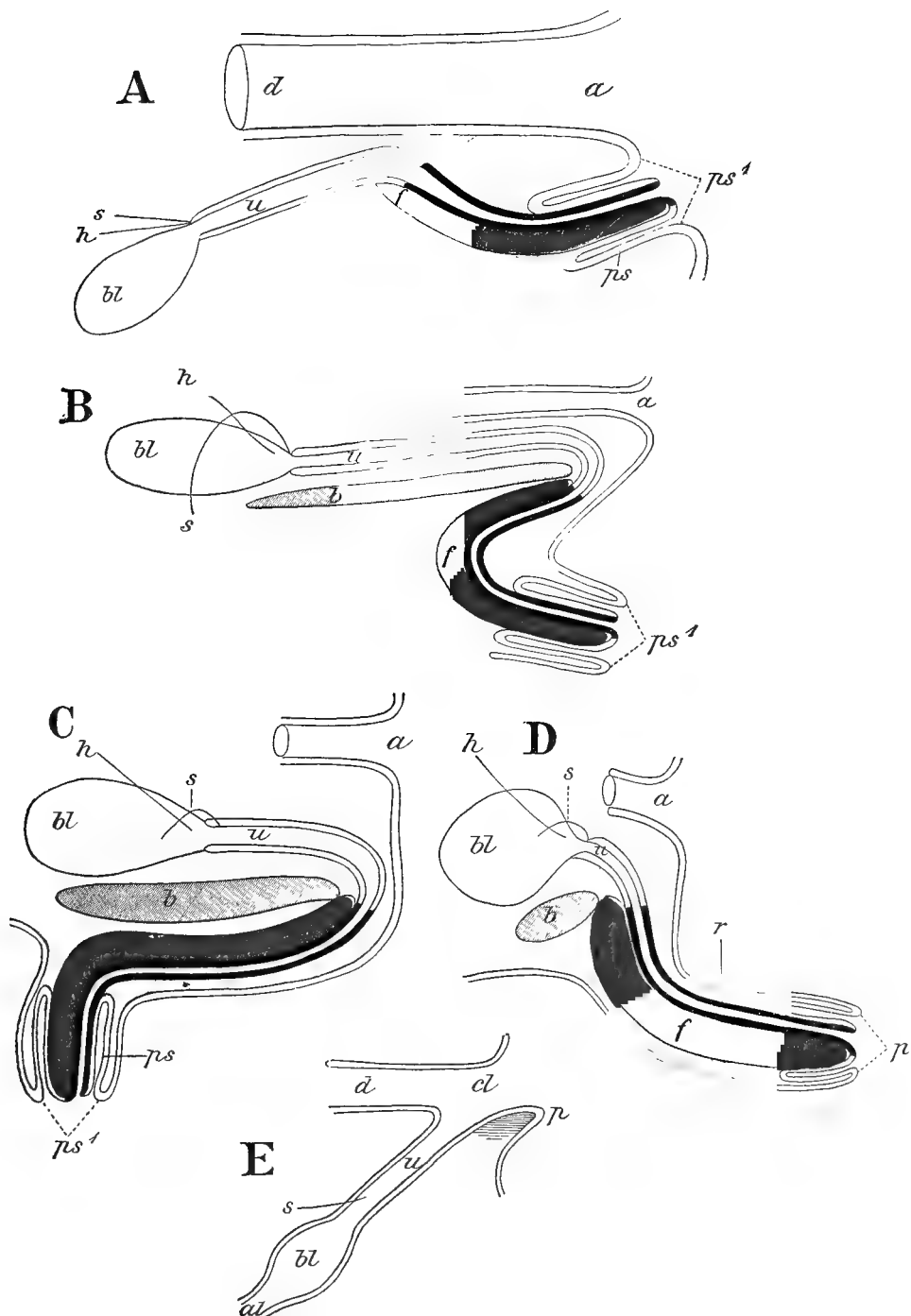
FIG. 306.—Continuation of Fig. 305. For description see next page.

Fig. 306.—(The special thickening of the corpus spongiosum and the glans penis present in some Mammals is not indicated).

A, *Marsupial* (very diagrammatic, for comparison with Fig. 305 C ; the obliterated opening of the urinogenital canal into the cloaca is indicated by dotted lines); B, Rodent (*Cœlogenys paca*) ; C, *Ape* (*Cercopithecus*): in most placental Mammals the apex of the penis does not hang down ; D, *Man* ; E, *Human fœtus*. Additional letterings : *a*, anus ; *b*, pelvic symphysis ; *p*, genital prominence, which gives rise to the penis or clitoris ; *al*, stalk of allantois.

ventral wall of the cloaca.    A channel passes along the side facing the cloaca to the opening of the urinogenital sinus: this condition is usually retained throughout life in the case of the clitoris of the female, while in the male (and occasionally in the female also) the groove becomes closed to form a canal continuous with the urinogenital canal or urethra, which thus becomes considerably lengthened.    In addition to the paired erectile corpora cavernosa there is a median *corpus spongiosum* or *corpus cavernosum urethræ* in connection with the penis (Fig. 307): corpora cavernosa are also
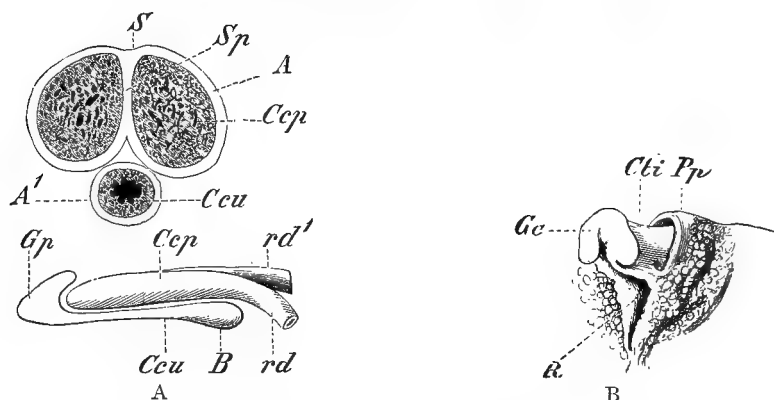


Fig. 307.—A, Semidiagrammatic Figure of the Human Penis.    (In transverse section and from the side.)  B, Clitoris of a Monkey (*Cebus capucinus*).

*A*, albuginea penis ; *A*[1], albuginea urethræ ; *Sp*, septum between the two corpora cavernosa ; *S*, sulcus dorsalis penis ; *Ccp*, corpus cavernosum ; *Ccu*, corpus spongiosum, which gives rise to the glans penis at *Gp*, and forms an oval enlargement (bulbus) at *B* ; *rd*, *rd*[1], crura of the corpora cavernosa ; *Cli*, clitoris, with its ventral furrow (*R*), glans (*Gc*), and prepuce (*Pp*).

present in the clitoris, and the corpus spongiosum, which retains its paired character, is represented by the so-called bulbi vestibuli at the vulva or entrance to the vagina.

In many Mammals a bone (*os penis*) becomes developed in the septum between the corpora cavernosa (*e.g.*, many Marsupials, Rodents, Bats, Carnivores, Whales, Lemurs, and Apes).    In some (*e.g.*, Seal) there is an *os clitoridis* in the female also.    The glans is provided with a special kind of tactile corpuscles, and in the male may bear horny papillæ and even calcified plates and spines (*e.g ,* certain Rodents).

In addition to the glandular vesiculæ seminales and the prostate (Fig. 377), paired *Cowper's glands* (Fig. 299), open in the male into the urinogenital canal, and representatives of these (*glands of Bartholini*) usually occur in the female. *Preputial glands* are also present between the prepuce and glans penis and in a corresponding position in the female.

## SUPRARENAL BODIES.

The *suprarenals* or *adrenals* are bodies of a glandular structure situated in the cœlome right and left of the vertebral column, generally in close proximity to the kidneys.

Nothing is known of these bodies in Amphioxus or in the Dipnoi. In Cyclostomes they are said to be present and to arise in connection with the anterior part of the pronephros. In Elasmobranchii and Holocephali they are represented by two distinct sets of structures—paired or unpaired *interrenals* of a yellow colour, close to the kidneys (Fig. 290), and a segmentally arranged row of *suprarenal* bodies, situated close to the inter-costal arteries in the neighbourhood of the kidneys. The former apparently represent the cortical (mesoblastic) and the former the medullary (epiblastic) portions of the adrenals of higher forms. In Teleostei the adrenals are usually paired and are in close relation with the kidneys—they correspond to the interrenals of Elasmobranchs. Amongst Ganoids the Sturgeon possesses numerous yellow bodies of the same nature. In Amphibia these organs form yellow streaks or dots on the ventral surface or inner border of the kidneys, receiving blood from the renal portal veins as well as from the renal arteries.

In the higher Vertebrates the adrenals consist of "cortical" and "medullary" portions, the latter derived from the sympathetic nervous system, and therefore epiblastic, and the former from the pronephros or mesonephros, or from the germinal epithelium (mesoblastic): the mode of development of the cortical substance, however, requires further investigation. They are abundantly supplied with blood-vessels and must have an important function, but their physiology is not understood. In Reptiles and Birds they are elongated and lobulated, and are situated close to the gonads. Both medulla and cortex are apparently represented in all these forms, but the relative relations of the two parts vary greatly. In Mammals each adrenal forms a definite and uniform rounded or oval mass lying near the corresponding kidney (Fig. 285 B), the medullary substance being central, and the cortical substance peripheral. In many Mammals these organs contain pigment cells as well as numerous lymphatic follicles and vessels.

C C

# APPENDIX

# APPENDIX.

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(*The abbreviations used in the following pages are given in brackets.*)

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